VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 2: 133–157
doi: 10.3897/VCS/2021/68594

RESEARCH PAPER

CLASSIFICATION OF OPEN HABITATS IN THE PALAEARCTIC

Xeric grasslands of the inner-alpine dry valleys of Austria – new insights into syntaxonomy, diversity and ecology

Martin Magnes[1], Wolfgang Willner[2], Monika Janišová[3], Helmut Mayrhofer[1], Elías Afif Khouri[4], Christian Berg[1], Anna Kuzemko[5], Philipp Kirschner[6], Riccardo Guarino[7], Harald Rötzer[8], Elena Belonovskaya[9], Asun Berastegi[10], Idoia Biurrun[11], Itziar Garcia-Mijangos[11], Ermin Mašić[12], Jürgen Dengler[13,14,15], Iwona Dembicz[16]

1 *Division of Plant Sciences, Institute of Biology, Karl-Franzens-University of Graz, Graz, Austria*
2 *Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria*
3 *Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences, Banská Bystrica, Slovakia*
4 *Department of Organisms and Systems Biology, Polytechnic School of Mieres, Oviedo University, Mieres, Spain*
5 *Geobotany and Ecology Department, M.G. Kholodny Institute of Botany, NAS of Ukraine, Kyiv, Ukraine*
6 *Department of Botany, University of Innsbruck, Innsbruck, Austria*
7 *Department STEBICEF – Botanical Unit, University of Palermo, Palermo, Italy*
8 *AVL Agency for Vegetation Ecology and Landscape Planning, Vienna, Austria*
9 *Department of Biogeography, Institute of Geography, Russian Academy of Sciences, Moscow, Russia*
10 *Department of Biodiversity, Environmental Management of Navarre, Pamplona-Iruña, Spain*
11 *Department of Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country UPV/EHU, Bilbao, Spain*
12 *Department of Biology, Faculty of Science, University of Sarajevo, Sarajevo, Bosnia and Herzegovina*
13 *Vegetation Ecology, Institute of Natural Resource Sciences (IUNR), Zurich University of Applied Sciences (ZHAW), Wädenswil, Switzerland*
14 *Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), Bayreuth, Germany*
15 *German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena, Leipzig, Germany*
16 *Department of Ecology and Environmental Conservation, Institute of Environmental Biology, Faculty of Biology, University of Warsaw, Warsaw, Poland*

Corresponding author: Martin Magnes (martin.magnes@uni-graz.at)

Academic editor: Arkadiusz Nowak ♦ **Received** 12 May 2021 ♦ **Accepted** 2 September 2021 ♦ **Published** 1 October 2021

Abstract

Aims: We studied the syntaxonomic position, biodiversity, ecological features, nature conservation value and current status of dry grasslands investigated by Josias Braun-Blanquet more than 60 years ago. **Study area**: Inner-alpine valleys of Austria. **Methods**: We sampled 67 plots of 10 m^2, following the standardized EDGG methodology. We subjected our plots to an unsupervised classification with the modified TWINSPAN algorithm and interpreted the branches of the dendrogram syntaxonomically. Biodiversity, structural and ecological characteristics of the resulting vegetation units at association and order level were compared by ANOVAs. **Results**: All the examined grasslands belong to the class *Festuco-Brometea*. From ten distinguished clusters, we could assign four clusters to validly published associations, while the remaining six clusters were named tentatively. We classified them into three orders: *Stipo-Festucetalia pallentis* (*Armerio elongatae-Potentilletum arenariae*, *Phleo phleoidis-Pulsatilletum nigricantis*, *Medicago minima-Melica ciliata* community, *Koelerio pyramidatae-Teucrietum montani*), *Festucetalia valesiacae* (*Sempervivum tectorum-Festuca valesiaca* community); *Brachypodietalia pinnati* (*Astragalo onobrychidis-Brometum erecti*, *Agrostis capillaris-Avenula adsurgens* community, *Anthericum ramosum-Brachypodium pinnatum* community, *Ranunculus bulbosus-Festuca rubra* community, *Carduus defloratus-Brachypodium pinnatum* community). **Conclusions**: The ten distinguished dry grassland communities of the Austrian inner-alpine valleys differ in their ecological affinities as well as their vascular plant, bryophyte and lichen diversity. We point out their high nature conservation importance, as each of them presents a unique habitat of high value.

PENSOFT.

Copyright *Martin Magnes et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Taxonomic reference: Names of vascular plants, bryophytes and lichens follow Fischer et al. (2008), Frahm and Frey (2004) and Nimis et al. (2018), respectively.

Syntaxonomic reference: Names of orders and classes follow Mucina et al. (2016), references for associations and alliances are given in the text.

Abbreviations: ANOVA = analysis of variance; DCA: detrended correspondence analyses; EDGG: Eurasian Dry Grassland Group; EIV: ecological indicator value; FL: Fließ; GR: Griffen; GU: Gulsen; KA: Kaunerberg; LA: Laudegg castle in Ladis; MA: Marin; NM: Neumarkt in der Steiermark; OM: Obermauern; PÖ: Pöls; PU: Puxer Loch; TWINSPAN = Two-way indicator species analysis; ZS: Zinizachspitze.

Keywords

Austria, biodiversity, *Brachypodietalia pinnati*, *Festucetalia valesiacae*, *Festuco-Brometea*, inner-alpine dry valley, semi-natural grassland, soil parameter, resurvey, *Stipo-Festucetalia pallentis*, syntaxonomy, vegetation classification

Introduction

The European Alps ("Alps") form a nearly 1,200 km long arc from Nice in the southwest to Vienna in the northeast, with the widest sector in the centre of the Eastern Alps, stretching approximately 240 km from north to south (Ozenda 1988). The Alps represent a biodiversity hotspot in Central Europe, with 4,491 observed vascular plant species (Aeschimann et al. 2004; Barthlott et al. 2005). The inner-alpine valleys are the central parts of the great longitudinal valleys between the highest ridges of the Alps and represent islands of continentality within the relatively oceanic climate of the mountain ranges. One important aspect of continentality is the low precipitation, caused by the high altitudes of the mountains that cast rain shadows towards the south and southeast, leeward of the prevailing rain-bringing northwestern winds. While even the driest parts of the Alps are more humid than true steppes (Ozenda 1988), these valleys provide refugial habitats to many species with a distribution centred in the steppe biome of Eastern Europe (Kirschner et al. 2020). Similar intra-montane valleys with continental climate and *Festuco-Brometea* grasslands are known from other high mountain ranges, like the Caucasus (Belonovskaya et al. 2016).

The inner valleys of the Alps have been inhabited by humans since the Bronze Age (Sydow 1995; Bätzing 2005) or even earlier (Patzelt 1996), up to elevations exceeding 2,000 m (Braun-Blanquet 1961; Schwabe and Kratochwil 2012). Therefore, the contemporary landscape has been influenced by millennia of land use, mainly as pastures and meadows. It is evident that the traditional agro-pastoral practice exerted a positive feedback on the *Festuco-Brometea* grasslands, as already noticed by Braun-Blanquet (1961), who described the succession from the *Astragalo-Brometum* to *Larix decidua* or *Pinus sylvestris* forests after the cessation of management. Both the isolated relic character of these steppe elements and the requirement of adequate management underline the need of skilled nature protection measures in these unique habitats. Phytosociological studies are well suited for evidence-based decisions in nature conservation. However, most studies of the inner-alpine dry valleys (Buschardt 1979; Wagner 1979; Schwabe and Kratochwil 2004, 2012; Wiesner et al. 2015; Dengler et al. 2019) focused on the more (south)western parts of the Alps with a severe summer drought, and merely touched the Eastern Alps, which have only a moderately continental climate that is influenced by cyclones from the Adriatic Sea.

Our study is part of a long-term project of the Eurasian Dry Grassland Group (EDGG) that will cover the inner-alpine dry grasslands in the whole Alps (Dengler et al. 2020a; Magnes et al. 2020). In the present paper, we focus on the dry grassland vegetation of the inner-alpine valleys of the Austrian Alps, revisiting sites that were already described by Braun-Blanquet (1961). More specifically, we provide a preliminary syntaxonomic classification using modern multivariate methods, describe the biodiversity and ecology of these grasslands and discuss their conservation management.

Study area

We mainly sampled in three regions of Austria: the Upper Inn valley in North Tyrol, the Virgen valley in East Tyrol and the central Mur valley in Styria. Additionally, one site in the Carinthian Basin was visited (Figure 1). Aridity is most pronounced in the Upper Inn valley (Magnes et al. 2018), and although Landeck is located highest among the three weather stations presented (Figure 2), the annual mean temperature is higher and annual precipitation is lower than at stations in the other two.

Upper Inn valley

Sampling localities: Fließ (FL), Kaunerberg (KA), Laudegg castle in Ladis (LA) (Figure 1).

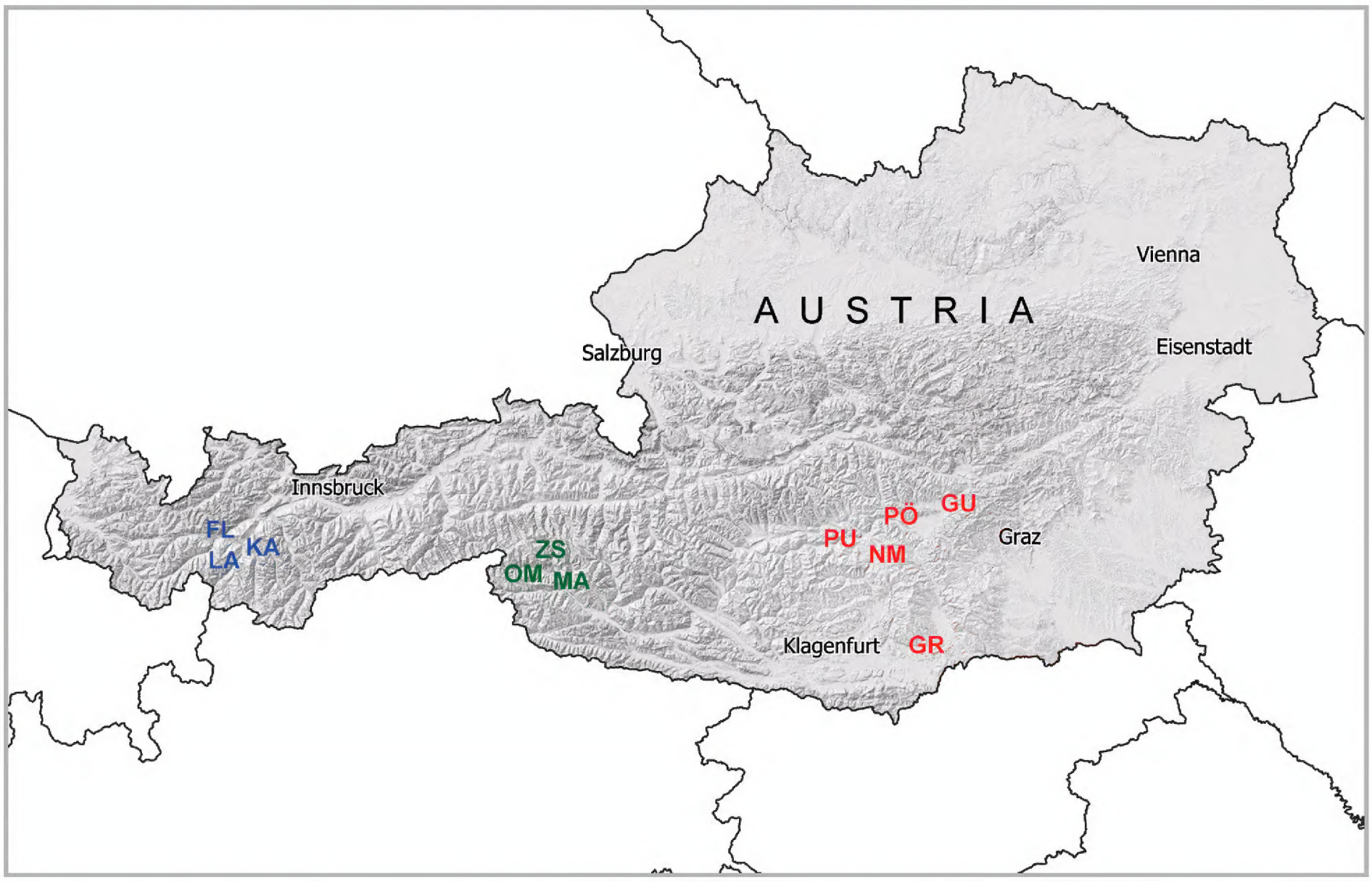
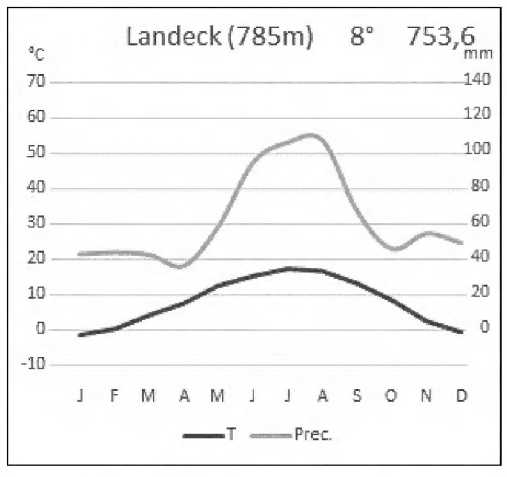
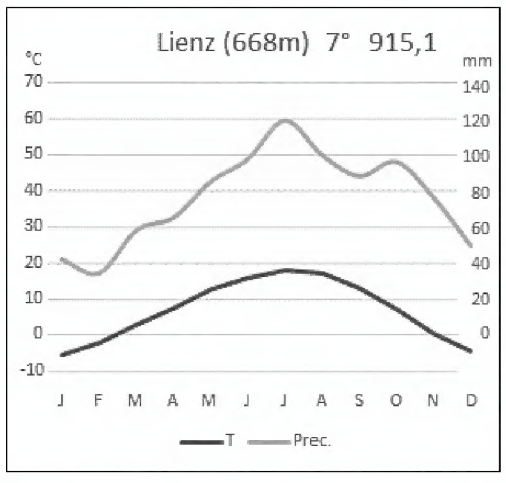


Figure 1. Location of the study sites: blue: Upper Inn valley (FL: Fließ, LA: Laudegg castle in Ladis, KA: Kaunerberg); green: Virgen valley (OM: Obermauern, ZS: Zinizachspitze, MA: Marin), red: Mur valley and Carinthian Basin (PU: Puxer Loch, NM: Neumarkt in der Steiermark, PÖ: Pöls, GR: Griffen, GU: Gulsen).





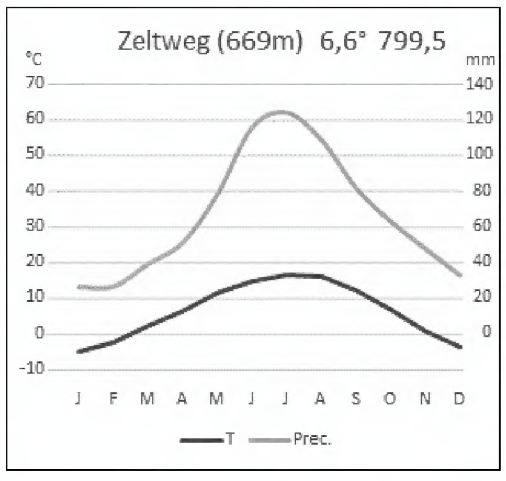


Figure 2. Climate diagrams from weather stations adjacent to the study sites (from west to east): The Upper Inn valley (Landeck), East Tyrol (Lienz, the closest ZAMG climate station to the Virgen valley), and the Mur valley (Zeltweg), based on data period 1971–2000 (ZAMG 2020). T: mean monthly temperature, Prec.: mean monthly precipitation.

The sampling was performed in the Nature Park Kaunergrat, southwest of Landeck, in one of the driest regions of the Austrian Alps. Our study area is close to the Engadin in Switzerland and the most continental area of the Eastern Alps, the Vinschgau in South Tyrol (Italy). Braun-Blanquet (1961) described the dry grasslands of the Austrian Upper Inn Valley in conjunction with those of the Lower Engadin because of the proximity and the similarity in geology, climate and species composition.

Geologically, the Kaunerberg (KA) and the study sites below the castle Laudegg (LA) belong to the easternmost part of the Engadin window. Kauns-Kaunerberg is located above Bündner schist, a metamorphic marine sediment from the Cretaceous period that is rich in calcium carbonate (Gruber et al. 2010). In contrast, the study sites below the Laudegg castle are situated above a much older, Triassic bedrock of metamorphic quartzite sandstone (Gruber et al. 2010). However, both rock materials favoured the formation of shallow soils at these localities. Another process that had a large influence on the composition of the soils at the studied sites was the deposition of drift and moraine material by the Inn glacier during the Würm Glacial. In course of this, rocks from a wider glacial catchment (e.g. Bündner schists, but also dolomites) were distributed and deposited along the valley slopes. This propagated the

formation of calcareous soils at the study sites below Fließ (FL), although the bedrock below is exclusively made up of acidic mica schists of the Variscan Silvretta crystalline (Gruber et al. 2010).

The studied dry grassland sites bear witness of an old cultural landscape. Traditionally, these sites were communal pastures ("Allmende") for small livestock (mainly sheep, to a lesser amount goats) in spring and autumn, before and after summering on alpine pastures at higher elevations. This kind of management is documented back to the medieval ages, but likely is much older. Until the 1940s and early 1950s, several hundred animals were herded in the slopes below Fließ. However, this practice was abandoned alongside the economic upturn of the post-war era, leading to a reforestation of the sites. This negative trend lasted until 2002, when, following the long-lasting pressure of regional conservationists, the sites at Fließ were finally put under protection and integrated into the Natura 2000 network. The sites at Kauns-Kaunerberg followed shortly after and are protected under Tyrolean law since 2006. Since then, both sites have been managed by the Kaunergrat Nature Park. Management measures include the initial re-establishment of abandoned areas by removal of bushes and trees, and subsequent, targeted grazing by cattle, goats and sheep. Since their implementation, these activities have been regularly evaluated via monitoring studies on vegetation and selected insect taxa (butterflies, ants). The area is the best example of inner-alpine dry valleys in Austria concerning size and extent of dry and semi-dry grassland vegetation.

Virgen valley

Sampling localities: Obermauern (OM), Marin (MA), Zinizachspitze (ZS) (Figure 1).

The Virgen valley runs in a west-east direction south of the main ridge of the Alps. It is quite remote from modern traffic routes and accessible only from the east, following the Isel river upstream. Due to its position south of the giant mountain massif Großvenediger (3,662 m), the climate is rather dry with an average annual precipitation of about 900 mm. The nearest climate station (Lienz, 30 km to the southeast) shows sub-Mediterranean characteristics with a relatively low precipitation in late summer (Figure 2), while the precipitation in Virgen is probably significantly lower (Wagner 1979). The main settlements are found from 1,200 to 1,300 m. North of the valley the geological bedrock is dominated by the schist shell of the Upper Tauern Penninicum.

The valley has been populated since prehistoric times. *Triticum aestivum* was cultivated until the 1980s and up to an elevation of approximately 1,400 m. Cattle breeding is another important land use. Traditionally, the animals were brought across mountain passes to markets on the northern side of the main ridge (Oberwalder 1999). Since the 19th century, markets that are more distant have become relevant. The settlement structure in the valley is characterised by small villages surrounded by a structurally rich cultural landscape called "Virger Feldflur" (Michor 1999). Part of it are hedges with *Berberis vulgaris*, *Rosa* spp. and *Sorbus aucuparia*. The former arable fields were gradually transformed into grasslands, resulting in a saying in local dialect: "Virgn isch grin woagn" ("Virgen has become green") (Oberwalder 1999).

The montane and subalpine zones reach from the valley bottom up to more than 2,000 m. On the northern slopes, *Picea abies* forests are dominant. On the sunny southern slopes, the forests were replaced by grasslands centuries ago. The forest remnants are usually dominated by *Larix decidua* with low cover and are still used as reserve pastures for dry years. The often very steep slopes were not only grazed by cattle, sheep and goats, but also used as mountain hay meadows as farmers could not produce enough hay in the lower parts of the valley. Hay was used as forage in winter in addition to harvested leaves and straw. The mountain meadows, sometimes even above the timberline, were traditionally mown only every second year. They are situated in the neighbourhood of the mountain pastures, which are mainly used for young cattle (Oberwalder 1999).

The bedrock of the sampling localities is mainly calcareous slate, partly covered with moraine material, and only on the southern border of OM there is also some dark phyllite together with the calcareous slate (Frank et al. 1987).

Mur valley and Carinthian Basin

Sampling localities: Puxer Loch (PU), Neumarkt in der Steiermark (NM), Pöls (PÖ), Griffen (GR), Gulsen (GU) (Figure 1).

The studied part of the Mur valley is situated along the upper reaches of the river, approximately 80 to 120 km east of its source. Braun-Blanquet (1961) identified this area as the easternmost extension of the inner-alpine dry valleys. In comparison to the climate of Lienz (Figure 2), the precipitation is lower without a depression in late summer (Figure 2, climate station of Zeltweg). Additional to the two sites within the Mur valley itself (GU, PU), we include here plots in the area of an adjacent pass traversal (NM), one site in the Carinthian Basin (GR) and one site in a tributary valley of the Mur with the last population of the endemic *Stipa styriaca* (PÖ). The latter locality was not investigated by Braun-Blanquet (1961), because this species, probably a remnant of the glacial steppe-tundra, was discovered and described from this place only later (Melzer 1962; Martinovský 1970).

Although all sites are situated in the Austrian Central Alps, the geological bedrock is very diverse (Flügel and Neubauer 1984). While the westernmost site (PU) is located on a steep slope of Palaeozoic limestone (Murauer Palaeozoikum), the bedrock in NM consists of moraine material with quartzite. The habitat of *Stipa styriaca* in PÖ is a steep southern slope on black mica schist, and GU

is part of the greatest connected serpentinite outcrop of Central Europe (Brooks 1987), its steep southern slopes being one of the most peculiar habitats in Austria (Magnes 2018). The castle hill of Griffen (GR), a landmark visible for miles around, is an isolated block of marble (Gleirscher and Pacher 2005).

Methods

Vegetation and environmental data

In total, we sampled 67 plots of 10 m^2 (15 nested-plot series with two 10-m^2 subplots each and additional 37 normal plots, Suppl. materials 1, 2) with the EDGG methodology (Dengler et al. 2016) between the 6th and 13th July 2018. Each nested-plot series ("EDGG Biodiversity Plots") consists of a 100-m^2 plot, with nested series of 0.0001, 0.001, 0.01, 0.1, 1 and 10 m^2 in two opposite corners. All terricolous vascular plants, bryophytes and lichens were recorded with the shoot presence method (Dengler 2008) for all plot sizes, and their cover value in percent was estimated in the 10-m^2 plots.

Soil of the uppermost 10 cm was collected in each plot by mixing five random samples. The following soil parameters were measured (all measured environmental variables as header data are provided in Suppl. material 1): skeleton content (mass fraction of particles > 2 mm), percentages of sand, clay and silt, texture class estimated with Robinson pipette method after removing organic matter with 6% H_2O_2, field capacity (%), drainage rate (cm/h), available water (%), saturation (%), permanent wilting point (%), pH (in a suspension of 10 g dry soil in 25 ml aqua dest.), electrical conductivity (EC) (in a suspension of 10 g dry soil in 50 ml aqua dest., dS/m), organic matter (as loss at ignition at 430°C, %), organic carbon (%), N content estimated with the Kjeldahl method (%), C/N, available P (estimated with the Mehlich 3 method (PM3), mg/kg).

Other recorded environmental and structural parameters were (for methodological details, see Dengler et al. 2016): geographical position (with precision of 1 m), elevation (m), aspect (°), inclination (°), maximum microrelief (cm), soil depth (cm, mean of five measurements per plot), total vegetation cover (%), cover shrub layer (%), cover herb layer (%), cover bryophyte/lichen layer (%), cover litter (%), cover stones and rocks (%), cover gravel (%), cover fine soil (%), maximum height of shrubs (m), maximum height of herbs (cm), height of herb layer (mean of five measurements per plot), relief (topographic) position, and land use, with indication of grazing, mowing, burning or abandonment. For each relevé, mean ecological indicator values for temperature, continentality, light, moisture, nutrients and soil reaction were calculated in the JUICE 7.1 software (Tichý 2002), based on the values published by Ellenberg et al. (1991).

The complete data are stored in and available from the GrassPlot database (Dengler et al. 2018; Biurrun et al. 2019; https://edgg.org/databases/GrassPlot) as data-set AT_E. The 10-m^2 plots are also provided in Suppl. material 1 (header data) and Suppl. material 2 (sorted relevé table).

Data analysis

The compositional data, along with the header data, were entered into TURBOVEG (Hennekens and Schamineé 2001) and then imported into the program JUICE (Tichý 2002). Prior to the numerical analysis, occurrences of species in the shrub and herb layer were combined, using the formula of Fischer (2015). We conducted a TWINSPAN (Two-Way Indicator Species Analysis; Hill 1979) in the modified version proposed by Roleček et al. (2009), with the following settings: three pseudospecies cut levels (0%, 5% and 25%); total inertia as measure of heterogeneity; minimum group size: 2.

We tried cluster numbers up to 15 and finally selected the solution with 11 clusters as the basis for our classification, as it corresponded most closely to what we consider the association level. One cluster containing a single relevé was joined with another cluster, so finally ten relevé groups were distinguished. Moreover, three clusters were subdivided into regional variants. These variants partly corresponded to TWINSPAN clusters of finer resolution, but the assignment of relevés to regional variants was based on their geographical distribution.

Fidelity of species to relevé groups was calculated using the phi coefficient of association (Chytrý et al. 2002), assuming equal cluster size (Tichý and Chytrý 2006). To provide diagnostic species both at order and association level, the calculations were done in Excel, which precluded the application of Fisher's exact test. However, we set phi-value thresholds so high that essentially no non-significant species were chosen at the association level. Species were considered as diagnostic with phi ≥ 0.25 at order level and phi ≥ 0.45 at association level. Additionally, we required in both cases that the drop in phi-value to the syntaxon with the next highest phi-value was at least 0.25; otherwise, the species was also considered diagnostic in the latter syntaxon. If such a drop of 0.25 did not occur anywhere in the sequence of syntaxa ordered by decreasing phi-values, a species was considered not diagnostic. If a species was diagnostic at both order and association level, it was assigned to the level where the phi-value was higher, provided all other conditions were fulfilled. The term "diagnostic species" is used here in a data-set specific context and should not be understood as equivalent to character species (see Willner et al. 2009).

We tried to assign our relevé groups to phytosociological associations, alliances and orders described in the literature by comparing the species composition. If such an assignment was ambiguous, we used informal community names. We refrained from formally describing new syntaxa, as this will be the task of a future, more comprehensive revision of all dry grasslands of the Eastern Alps. To facilitate the syntaxonomic interpretation, we

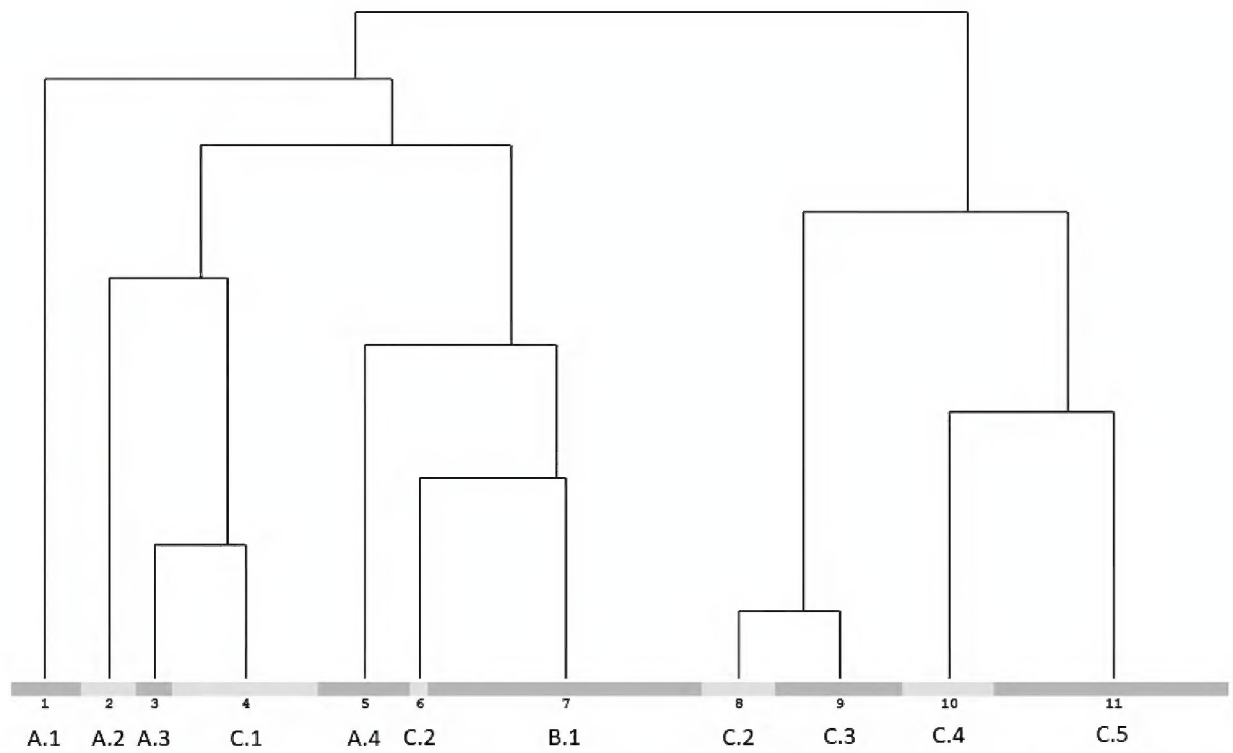


Figure 3. Dendrogram of the 11-cluster resolution from modified TWINSPAN analysis. Below the cluster numbers, the corresponding association/community is indicated (A.1–A.4: *Stipo-Festucetalia pallentis*, B.1: *Festucetalia valesiacae*, C.1–C.5: *Brachypodietalia pinnati*). For the meaning of the community codes, see text.

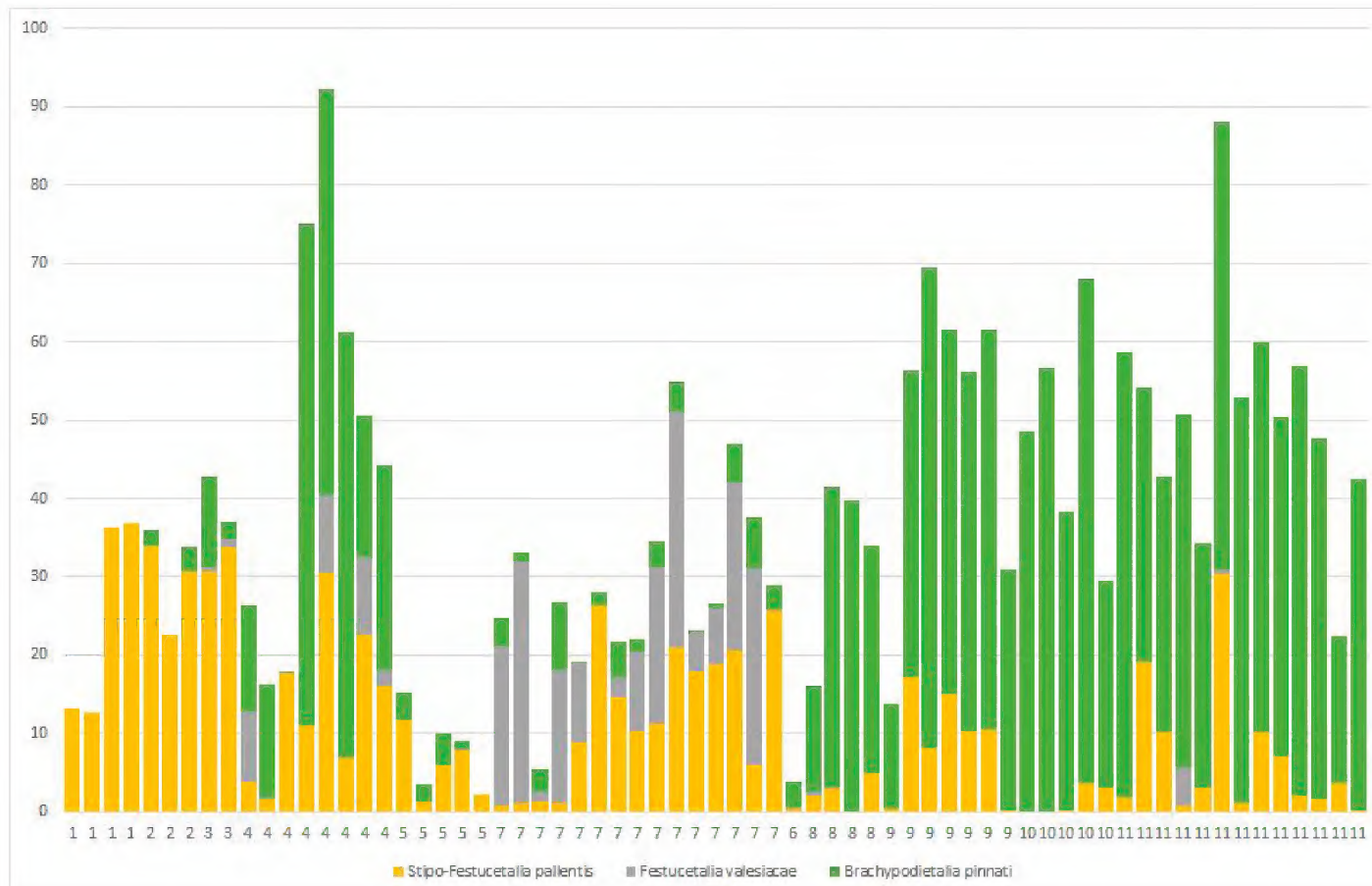


Figure 4. Stacked total percentage covers of the diagnostic species of the orders *Stipo-Festucetalia pallentis* (A), *Festucetalia valesiacae* (B) and *Brachypodietalia pinnati* (C) in each relevé. The numbers below the diagram are the TWINSPAN clusters. The sequence of the relevés is the same as in Figure 3 but differs from Table 1 in the position of cluster 4. Note that the percentage cover of non-diagnostic species is not shown.

calculated for each relevé the total percentage cover of the diagnostic species of orders according to Willner et al. (2019) using the function "total cover of <colour> species" in JUICE.

To visualize the relation of the species composition of the relevé groups (and relevés) to measured or calculated factors we performed a DCA using Canoco 5 (ter Braak and Šmilauer 2012) with downweighting of rare species and log-transformation of cover values.

The number and cover of red list species were calculated in JUICE based on Niklfeld and Schratt-Ehrendorfer (1999) for vascular plants, Grims and Köckinger (1999) and Saukel and Köckinger (1999) for bryophytes and Türk and Hafellner (1999) for lichens.

Results

Numerical classification

The first TWINSPAN division resulted in two groups roughly corresponding to the orders *Stipo-Festucetalia pallentis* (clusters 1–7) and *Brachypodietalia pinnati* (clusters 8–11) of the class *Festuco-Brometea* (Figure 3). Cluster 4 was transitional between the two orders, with most of its relevés having a higher total cover of *Brachypodietalia* species (Figure 4). Cluster 7 was transitional between the *Stipo-Festucetalia pallentis* and *Festucetalia valesiacae* with several relevés clearly belonging to the latter order (Figure 4). Cluster

6, containing a single relevé, showed a clear prevalence of *Brachypodietalia* species (Figure 4). As it shared several otherwise rare species with cluster 8 (e.g., *Allium carinatum*, *Avenula adsurgens*, *Jasione montana*, *Potentilla argentea*), and the relevés of both clusters were from the same location, we joined these two clusters into a single community. Otherwise, we refrained from moving single relevés between clusters based on their affinity to phytosociological orders, but potentially misclassified relevés are mentioned in the description of the individual communities.

Therefore, we classified our relevés into ten vegetation units at association level, which in turn were grouped in the three orders (A) *Stipo-Festucetalia pallentis*, (B) *Festucetalia valesiacae* and (C) *Brachypodietalia pinnati* (Table 1, Suppl. material 2). The alliance level remained unresolved (see Discussion).

Table 1. Abridged synoptic table of the associations, based on the 10-m² plots. For each syntaxon, the 10 species with the highest phi-values are shown plus all species with 10% or higher constancy across all plots. The number of presented vs. total species in each group is given in brackets. Values are percentage constancies. Species are sorted by decreasing fidelity within the respective syntaxon and by decreasing overall constancy in case of accompanying species. The complete synoptic and relevé table is provided in Suppl. material 2. B: bryophyte, L: lichen, V: vascular plant.

Syntaxon		All	A	B	C	A.1	A.2	A.3	A.4	B.1	C.1	C.2	C.3	C.4	C.5
Number of plots		**67**	**14**	**15**	**38**	**4**	**3**	**2**	**5**	**15**	**8**	**5**	**7**	**5**	**13**
Diagnostic species order A (3)															
Hypnum cupressiforme	B	16	43	7	11	50	.	50	60	7	.	20	14	20	8
Geranium columbinum	V	7	21	.	5	.	33	50	20	.	13	20	.	.	.
Echium vulgare	V	4	14	.	3	.	33	50	.	.	.	.	14	.	.
Diagnostic species association A.1 (11 of 15)															
Alyssum montanum	V	6	29	.	.	100	.	.	.	.	.	.	.	.	.
Asplenium cuneifolium	V	6	29	.	.	100	.	.	.	.	.	.	.	.	.
Dorycnium germanicum	V	6	29	.	.	100	.	.	.	.	.	.	.	.	.
Koeleria pyramidata var. *pubiculmis*	V	6	29	.	.	100	.	.	.	.	.	.	.	.	.
Potentilla incana	V	6	29	.	.	100	.	.	.	.	.	.	.	.	.
Festuca pallens	V	7	29	.	3	100	.	.	.	.	.	.	14	.	.
Lepraria lobificans	L	4	21	.	.	75	.	.	.	.	.	.	.	.	.
Erysimum sylvestre	V	15	50	13	3	100	.	.	60	13	13	.	.	.	.
Jovibarba globifera subsp. *hirta*	V	6	21	.	3	75	.	.	.	.	.	20	.	.	.
Notholaena marantae	V	3	14	.	.	50	.	.	.	.	.	.	.	.	.
Weissia brachycarpa	B	12	21	7	11	75	.	.	.	7	25	.	.	.	15
Diagnostic species association A.2 (10 of 13)															
Alliaria petiolata	V	3	14	.	.	.	67	.	.	.	.	.	.	.	.
Myosotis ramosissima	V	3	14	.	.	.	67	.	.	.	.	.	.	.	.
Origanum vulgare	V	10	21	.	11	.	100	.	.	.	.	.	57	.	.
Fallopia convolvulus	V	10	21	.	11	.	100	.	.	.	.	60	14	.	.
Stachys recta	V	12	29	.	11	.	100	50	.	.	13	.	43	.	.
Scabiosa ochroleuca	V	6	14	.	5	.	67	.	.	.	.	.	29	.	.
Teucrium chamaedrys	V	19	21	13	21	.	100	.	.	13	38	20	57	.	.
Aster amellus	V	12	14	27	5	.	67	.	.	27	25	.	.	.	.
Bromus inermis	V	1	7	.	.	.	33	.	.	.	.	.	.	.	.
Galeopsis pubescens	V	1	7	.	.	.	33	.	.	.	.	.	.	.	.
Diagnostic species association A.3 (10 of 15)															
Medicago minima	V	10	14	20	5	.	.	100	.	20	25	.	.	.	.
Agrimonia eupatoria	V	12	14	.	16	.	.	100	.	.	25	.	57	.	.
Amblystegium serpens	B	1	7	.	.	.	.	50	.	.	.	.	.	.	.
Clinopodium nepeta agg.	V	1	7	.	.	.	.	50	.	.	.	.	.	.	.
Erigeron acris	V	1	7	.	.	.	.	50	.	.	.	.	.	.	.
Lapsana communis	V	1	7	.	.	.	.	50	.	.	.	.	.	.	.
Silene latifolia	V	1	7	.	.	.	.	50	.	.	.	.	.	.	.
Torilis arvensis	V	1	7	.	.	.	.	50	.	.	.	.	.	.	.
Melica ciliata	V	18	21	40	8	.	33	100	.	40	38	.	.	.	.
Artemisia absinthium	V	3	7	7	.	.	.	50	.	7	.	.	.	.	.
Galium lucidum	V	24	36	33	16	.	33	100	40	33	50	.	14	.	8
Diagnostic species association A.4 (12 of 19)															
Poa badensis agg.	V	9	36	7	.	.	.	.	100	7	.	.	.	.	.
- *Poa molinieri*		4	14	7	.	.	.	.	40	7	.	.	.	.	.
Toninia sedifolia	L	6	29	.	.	.	.	.	80	.	.	.	.	.	.
Tortella inclinata	B	6	29	.	.	.	.	.	80	.	.	.	.	.	.
Ditrichum flexicaule	B	7	29	.	3	.	.	.	80	.	.	.	.	20	.
Peltigera rufescens	L	7	29	.	3	.	.	.	80	.	.	.	.	20	.
Saxifraga paniculata	V	4	21	.	.	.	.	.	60	.	.	.	.	.	.
Psora decipiens	L	6	21	7	.	.	.	.	60	7	.	.	.	.	.
Cladonia symphycarpa	L	15	29	40	.	.	.	.	80	40	.	.	.	.	.
Physconia muscigena	L	7	21	13	.	.	.	.	60	13	.	.	.	.	.
Cladonia macrophyllodes	L	3	14	.	.	.	.	.	40	.	.	.	.	.	.
Endocarpon pusillum	B	10	21	27	.	.	.	.	60	27	.	.	.	.	.
Tortella tortuosa	B	22	29	40	13	.	.	.	80	40	.	.	.	20	31
Diagnostic species order B (21 of 35)															
Festuca valesiaca	V	33	14	93	16	.	.	50	20	93	38	.	.	20	15
Sempervivum tectorum	V	16	.	67	3	.	.	.	.	67	13	.	.	.	.

Syntaxon		All	A	B	C	A.1	A.2	A.3	A.4	B.1	C.1	C.2	C.3	C.4	C.5
Number of plots		**67**	**14**	**15**	**38**	**4**	**3**	**2**	**5**	**15**	**8**	**5**	**7**	**5**	**13**
Veronica spicata	V	19	.	67	8	.	.	.	.	67	25	.	.	20	.
Artemisia campestris	V	39	50	100	11	.	67	.	100	100	50	.	.	.	.
Koeleria macrantha	V	22	14	73	5	25	33	.	.	73	25	.	.	.	.
Dianthus sylvestris	V	33	36	87	11	.	.	.	100	87	25	.	.	40	.
Galium verum	V	31	7	73	24	.	.	50	.	73	75	.	.	60	.
Bromus erectus	V	39	7	80	34	.	.	50	.	80	100	.	14	40	15
Parmelia somloensis	L	13	.	47	5	.	.	.	.	47	.	40	.	.	.
Phleum phleoides	V	31	14	73	21	.	.	50	20	73	63	40	.	20	.
Tortula ruralis	B	19	14	60	5	.	.	.	40	60	13	20	.	.	.
Potentilla pusilla	V	48	43	93	32	.	.	50	100	93	63	.	.	60	31
Petrorhagia saxifraga	V	24	21	67	8	.	.	.	60	67	38	.	.	.	.
Sempervivum arachnoideum	V	19	21	60	3	.	.	.	60	60	.	.	.	20	.
Vincetoxicum hirundinaria	V	45	14	80	42	.	67	.	.	80	100	20	86	20	.
Sedum album	V	28	43	73	5	.	33	.	100	73	25	.	.	.	.
Festuca guestfalica	V	15	.	40	11	.	.	.	.	40	38	.	.	20	.
Sedum sexangulare	V	21	21	53	8	.	.	.	60	53	13	.	.	40	.
Hedwigia ciliata	L	16	7	40	11	.	.	50	.	40	.	60	.	20	.
Cladonia pyxidata	L	18	29	47	3	.	.	.	80	47	.	.	.	20	.
Scabiosa columbaria agg.	V	28	36	53	16	.	.	50	80	53	25	20	14	.	15
- Scabiosa columbaria		*13*	*29*	*13*	*8*	.	.	.	*80*	*13*	.	*20*	*14*	.	*8*
- Scabiosa lucida		*1*	.	.	*3*	.	.	.	.	.	.	.	.	.	*8*
- Scabiosa triandra		*13*	*7*	*40*	*5*	.	.	*50*	.	*40*	*25*	.	.	.	.
Diagnostic species order C (22 of 28)															
Leontodon hispidus	V	30	.	.	53	.	.	.	.	.	13	.	29	80	100
Achillea millefolium agg.	V	42	14	.	68	25	.	50	.	.	.	60	100	100	85
Lotus corniculatus	V	42	.	20	66	.	.	.	.	20	63	.	43	80	100
Dactylis glomerata	V	33	.	13	53	.	.	.	.	13	50	20	86	40	54
Veronica chamaedrys	V	18	.	.	32	.	.	.	.	.	.	60	43	80	15
Pimpinella saxifraga	V	30	14	.	47	.	.	50	20	.	.	20	71	60	69
- Pimpinella saxifraga subsp. nigra		6	.	.	*11*	.	.	.	.	.	.	.	*43*	.	*8*
Anthoxanthum odoratum agg.	V	16	.	.	29	.	.	.	.	.	.	20	14	60	46
Campanula glomerata	V	15	.	.	26	.	.	.	.	.	13	.	43	.	46
Cerastium holosteoides	V	12	.	.	21	.	.	.	.	.	.	.	14	40	38
Trifolium repens	V	12	.	.	21	.	.	.	.	.	13	20	14	40	23
Carex ornithopoda	V	10	.	.	18	.	.	.	.	.	.	.	.	40	38
Centaurea jacea	V	10	.	.	18	.	.	.	.	.	.	.	14	20	38
Galium pumilum	V	10	.	.	18	.	.	.	.	.	.	20	29	20	23
Larix decidua	V	10	.	.	18	.	.	.	.	.	.	.	.	40	38
Brachypodium pinnatum agg.	V	54	21	47	68	.	67	50	.	47	75	.	86	60	85
- Brachypodium pinnatum		*31*	*14*	.	*50*	.	*67*	.	.	.	.	.	*71*	*60*	*85*
- Brachypodium rupestre		*21*	*7*	*47*	*16*	.	.	*50*	.	*47*	*75*	.	.	.	.
Polygonatum odoratum	V	15	.	7	24	.	.	.	.	7	13	40	.	.	46
Fragaria vesca	V	15	7	.	24	.	.	50	.	.	13	20	57	60	.
Galium album	V	25	21	.	37	.	67	50	.	.	.	100	71	40	15
Koeleria pyramidata var. *pyramidata*	V	48	36	27	61	.	.	.	100	27	13	100	71	60	69
Seseli libanotis	V	18	7	7	26	.	.	50	.	7	38	.	43	.	31
Brachythecium rutabulum	B	12	7	.	18	.	.	50	.	.	13	20	14	20	23
Poa pratensis agg.	V	34	21	20	45	.	33	100	.	20	75	40	57	40	23
Diagnostic species association C.1 (2)															
Fragaria viridis	V	3	.	.	5	.	.	.	.	.	25	.	.	.	.
Astragalus onobrychis	V	9	.	20	8	.	.	.	.	20	38	.	.	.	.
Diagnostic species association C.2 (12 of 16)															
Potentilla argentea	V	10	.	13	13	.	.	.	.	13	.	100	.	.	.
Allium carinatum	V	10	.	7	16	.	.	.	.	7	.	100	14	.	.
Genista tinctoria	V	4	.	.	8	.	.	.	.	.	.	60	.	.	.
Jasione montana	V	4	.	.	8	.	.	.	.	.	.	60	.	.	.
Populus tremula	V	4	.	.	8	.	.	.	.	.	.	60	.	.	.
Potentilla rupestris	V	4	.	.	8	.	.	.	.	.	.	60	.	.	.
Avenula adsurgens subsp. *adsurgens*	V	15	7	.	24	.	33	.	.	.	.	100	43	.	8
Campanula rotundifolia	V	10	.	7	16	.	.	.	.	7	.	80	14	20	.
Viola arvensis	V	6	.	.	11	.	.	.	.	.	.	60	14	.	.
Ceratodon purpureus	B	7	.	7	11	.	.	.	.	7	13	60	.	.	.
Silene nutans	V	15	.	.	26	.	.	.	.	.	.	80	14	20	31
Cladonia fimbriata	B	12	7	13	13	25	.	.	.	13	.	60	.	20	8
Diagnostic species association C.3 (10 of 18)															
Anthericum ramosum	V	7	.	.	13	.	.	.	.	.	.	.	71	.	.
Campanula trachelium	V	7	.	.	13	.	.	.	.	.	.	.	71	.	.
Centaurea scabiosa	V	7	.	.	13	.	.	.	.	.	.	.	71	.	.
Tragopogon orientalis	V	7	.	.	13	.	.	.	.	.	.	.	71	.	.
Peucedanum oreoselinum	V	13	.	20	16	.	.	.	.	20	13	.	71	.	.
Astragalus glycyphyllos	V	9	7	.	13	.	33	.	.	.	.	.	71	.	.
Polygala comosa	V	4	.	.	8	.	.	.	.	.	.	.	43	.	.
Clinopodium vulgare	V	13	7	.	21	.	.	50	.	.	13	20	86	.	.
Viola hirta	V	16	7	.	26	.	.	50	.	.	38	.	86	.	8
Vicia cracca agg.	V	10	.	.	18	.	.	.	.	.	.	.	57	20	15
Diagnostic species association C.4 (11 of 19)															
Ranunculus bulbosus	V	9	.	.	16	.	.	.	.	.	.	.	14	100	.
Festuca rubra agg.	V	12	.	.	21	.	.	.	.	.	.	.	.	100	23

Syntaxon		All	A	B	C	A.1	A.2	A.3	A.4	B.1	C.1	C.2	C.3	C.4	C.5
Number of plots		**67**	**14**	**15**	**38**	**4**	**3**	**2**	**5**	**15**	**8**	**5**	**7**	**5**	**13**
- Festuca rubra		6	.	.	*11*	.	.	.	.	.	.	.	.	60	*8*
Knautia arvensis	V	4	.	.	8	.	.	.	.	.	.	.	.	60	.
Lolium perenne	V	4	.	.	8	.	.	.	.	.	.	.	.	60	.
Veronica officinalis	V	4	.	.	8	.	.	.	.	.	.	.	.	60	.
Calliergonella cuspidata	B	7	.	.	13	.	.	.	.	.	.	.	.	60	15
Ranunculus acris	V	7	.	.	13	.	.	.	.	.	.	.	.	60	15
Thuidium philibertii	B	7	.	.	13	.	.	.	.	.	.	.	.	60	15
Hieracium pilosella	V	25	.	27	34	.	.	.	.	27	.	40	.	100	46
Avenula pratensis	V	3	.	.	5	.	.	.	.	.	.	.	.	40	.
Plantago lanceolata	V	25	7	20	34	.	.	50	.	20	38	.	43	100	15
Diagnostic species association C.5 (21 of 55)															
Persicaria vivipara	V	13	.	.	24	.	.	.	.	.	.	.	.	.	69
Potentilla erecta	V	24	.	.	42	.	.	.	.	.	.	.	.	60	100
Phyteuma orbiculare	V	10	.	.	18	.	.	.	.	.	.	.	.	.	54
Plantago atrata	V	10	.	.	18	.	.	.	.	.	.	.	.	.	54
Ranunculus nemorosus	V	10	.	.	18	.	.	.	.	.	.	.	.	.	54
Thesium alpinum	V	15	.	.	26	.	.	.	.	.	.	.	.	20	69
Centaurea pseudophrygia	V	9	.	.	16	.	.	.	.	.	.	.	.	.	46
Gymnadenia conopsea	V	9	.	.	16	.	.	.	.	.	.	.	.	.	46
Laserpitium latifolium	V	9	.	.	16	.	.	.	.	.	.	.	.	.	46
Molinia caerulea	V	9	.	.	16	.	.	.	.	.	.	.	.	.	46
Pimpinella major	V	13	.	.	24	.	.	.	.	.	.	.	.	20	62
Polygala chamaebuxus	V	13	.	.	24	.	.	.	.	.	.	.	.	20	62
Carlina acaulis	V	27	.	7	45	.	.	.	.	7	.	.	29	60	92
Euphrasia officinalis	V	16	.	.	29	.	.	.	.	.	.	.	.	40	69
Galium anisophyllon	V	16	.	.	29	.	.	.	.	.	.	.	.	40	69
Carduus defloratus	V	19	7	.	32	25	.	.	.	.	13	.	.	20	77
Trifolium montanum	V	33	.	13	53	.	.	.	.	13	13	.	43	60	100
Campanula scheuchzeri	V	12	.	.	21	.	.	.	.	.	.	.	.	20	54
Sesleria caerulea	V	12	.	.	21	.	.	.	.	.	.	.	.	20	54
Anthyllis vulneraria	V	19	14	.	29	.	.	.	40	.	.	.	14	20	69
Hippocrepis comosa	V	12	.	.	21	.	.	.	.	.	13	.	.	20	46
Diagnostic species for more than one order (3)															
Carex caryophyllea	V	52	7	60	66	.	.	.	20	60	63	100	29	80	69
Allium lusitanicum	V	42	71	73	18	50	100	.	100	73	13	.	14	.	38
Thymus praecox	V	33	50	67	13	100	.	50	40	67	50	.	14	.	.
Diagnostic species for more than one association (18 of 25)															
Thymus pulegioides	V	37	29	20	47	.	.	.	80	20	25	.	.	80	92
Briza media	V	33	.	13	53	.	.	.	.	13	.	.	71	60	92
Salvia pratensis	V	31	7	60	29	.	.	50	.	60	63	.	86	.	.
Plantago media	V	25	.	7	42	.	.	.	.	7	38	.	.	60	77
Teucrium montanum	V	24	29	33	18	.	.	.	80	33	88	.	.	.	.
Agrostis capillaris	V	22	.	.	39	.	.	.	.	.	.	100	.	80	46
Trifolium pratense	V	22	7	.	37	.	.	50	.	.	.	.	14	100	62
Leucanthemum vulgare agg.	V	21	.	.	37	.	.	.	.	.	.	.	.	80	77
Linum catharticum	V	21	.	.	37	.	.	.	.	.	.	.	.	80	77
Verbascum chaixii subsp. *austriacum*	V	21	36	.	24	50	100	.	.	.	.	80	57	.	8
Arrhenatherum elatius	V	18	.	7	29	.	.	.	.	7	.	60	71	20	15
Taraxacum sect. *Ruderalia*	V	16	.	.	29	.	.	.	.	.	.	.	71	60	23
Primula veris	V	15	.	.	26	.	.	.	.	.	.	.	57	.	46
Hylotelephium maximum	V	13	29	.	13	75	33	.	.	.	.	100	.	.	.
Genista sagittalis	V	12	.	.	21	.	.	.	.	.	.	80	57	.	.
Homalotrichon (Avenula) pubescens	V	12	.	.	21	.	.	.	.	.	.	60	43	.	15
Prunella vulgaris	V	12	.	.	21	.	.	.	.	.	.	.	.	60	38
Trifolium arvense	V	12	7	27	8	.	.	50	.	27	.	60	.	.	.
Other species (22 of 209)															
Abietinella abietina	B	57	43	53	63	.	33	.	100	53	63	100	.	80	77
Euphorbia cyparissias	V	57	36	60	63	50	.	50	40	60	63	100	71	60	46
Carex humilis	V	55	57	73	47	75	100	100	.	73	88	20	29	.	62
Helianthemum nummularium subsp. *obscurum*	V	52	36	47	61	.	33	.	80	47	63	20	71	60	69
Festuca rupicola	V	48	50	27	55	.	100	.	80	27	38	100	86	60	31
Rhytidium rugosum	B	46	43	53	45	50	.	.	80	53	25	80	.	40	69
Medicago falcata	V	28	21	33	29	.	33	50	20	33	88	.	57	.	.
Bryum argenteum	B	18	21	27	13	.	.	.	60	27	13	60	.	20	.
Hypericum perforatum	V	16	14	.	24	25	33	.	.	.	.	40	71	40	.
Sanguisorba minor	V	16	7	13	21	.	33	.	.	13	38	.	43	40	.
Cuscuta epithymum	V	15	14	7	18	.	67	.	.	7	38	20	43	.	.
Arenaria serpyllifolia agg.	V	13	29	20	5	50	33	.	20	20	.	.	14	20	.
Asperula cynanchica	V	13	14	7	16	50	.	.	.	7	38	.	29	20	.
Medicago lupulina	V	13	14	.	18	.	33	.	20	.	13	.	29	20	23
Rosa canina agg.	V	12	14	7	13	.	33	50	.	7	25	20	29	.	.
Securigera varia	V	12	14	13	11	.	33	50	.	13	50	.	.	.	.
Cladonia furcata	L	10	.	13	13	.	.	.	.	13	.	20	.	.	31
Clinopodium alpinum	V	10	7	.	16	.	.	.	20	.	.	.	.	40	31
Didymodon rigidulus	B	10	14	27	3	.	.	.	40	27	.	.	.	20	.
Leucodon sciuroides	B	10	14	27	3	.	.	50	20	27	13	.	.	.	.
Prunus spinosa	V	10	7	.	16	.	.	50	.	.	25	40	29	.	.
Sedum acre	V	10	21	20	3	25	.	.	40	20	13	.	.	.	.

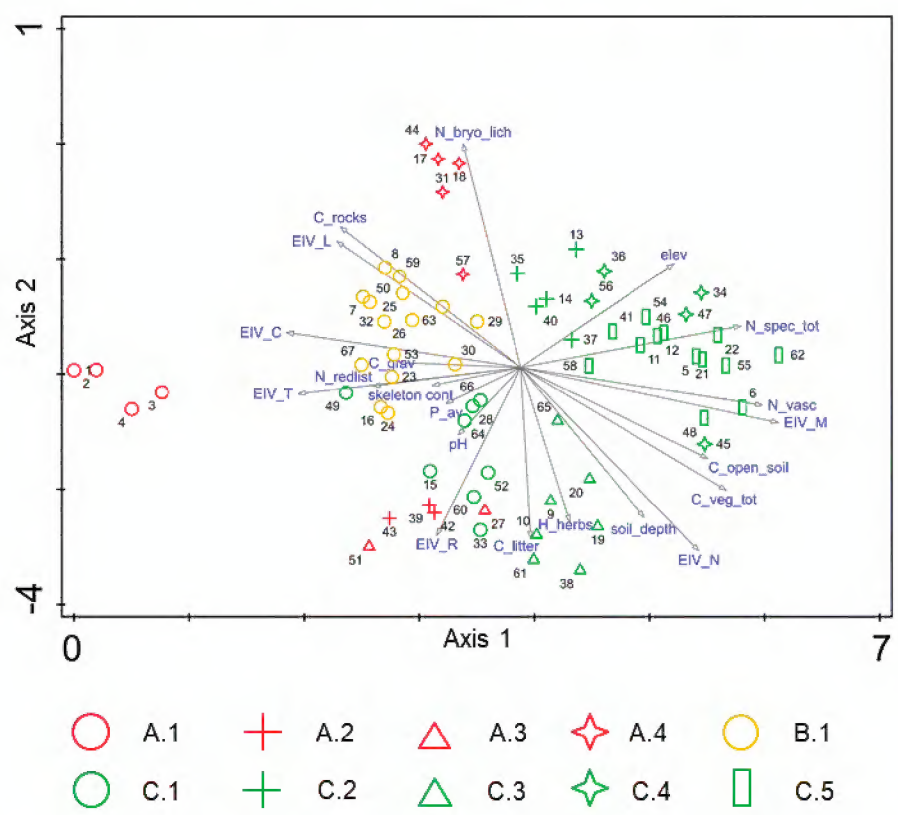


Figure 5. DCA of the 10-m² plots sampled during the 11th EDGG Field Workshop (gradient length/eigenvalue/cumulative explained variation of Axis 1: 6.12/0.646/8.56, Axis 2: 3.70/0.4086/13,97). A.1–C.5: clusters according to the order/association code in Table 1, Suppl. material 2: **red**: *Stipo-Festucetalia pallentis* (A), **yellow**: *Festucetalia valesiacae* (B), **green**: *Brachypodietalia pinnati* (C); **vectors**: **C_grav**: cover of gravel; **C_litter**: cover of litter; **C_open_soil**: cover open soil; **C_rocks**: cover of rocks and stones; **C_veg_ot**: total vegetation cover; **elev**: elevation; EIV_C: Ellenberg indicator value for continentality; EIV_L: Ellenberg indicator value for light; EIV_M: Ellenberg indicator value for moisture; EIV_N: Ellenberg indicator value for nutrients; EIV_R: Ellenberg indicator values for soil reaction; EIV_T: Ellenberg indicator values for temperature; **H_herbs**: maximum height of herbs; **N_bryo_lich**: species number of bryophytes and lichens; **N_redlist**: number of red-list species; **N_vasc**: number of vascular plant species; **N_grass**: number of grass species; **N_spec_tot**: total species number; **P_av**: available Phosphor; skeleton con: skeleton content. The numbers show the position of the plots (For TURBOVEG numbers, see Suppl. material 1).

Ordination

The first axis of the DCA graph (Figure 5) corresponds to a gradient of skeleton content and partly soil depth, supporting the division between the *Stipo-Festucetalia pallentis* (clusters A.1–A.4) on the left (high skeleton content, low soil depth) and the *Brachypodietalia pinnati* (clusters C.1–C.5) on the right, with cluster B.1 (*Festucetalia valesiacae*) in an intermediate position. Axis 2 depicts mainly litter cover, a good proxy for abandonment of management in the lower parts of the graph. The neatly grazed grassland of cluster A.4 (OM) in the upper part of the graph, having a high number of bryophytes and lichens, contrasts with the abandoned sites of PU and PÖ of clusters A.2 and A.3 having high litter cover and higher indicator values for nutrients.

Biodiversity and vegetation cover

Maximum species richness for all taxa increased from 9 in 0.0001 m² to 103 in 100 m² (Table 2). Across grain

Table 2. Scale-dependent species richness of the studied nested-plot series. We provide maximum values across all 15 nested-plot series and means ± standard deviation for each of the three distinguished orders. Number of samples is given in brackets (first number for grain sizes up to 10 m², second number for 100 m²).

Area [m²]	All Max.	Order A (n = 7/3)	B (n = 9/4)	C (n = 14/6)
All taxa				
0.0001	9	2.0 ± 2.0	2.1 ± 1.1	4.0 ± 1.9
0.001	11	3.0 ± 2.2	3.2 ± 1.6	6.6 ± 2.6
0.01	19	4.9 ± 2.4	5.6 ± 2.6	11.2 ± 3.9
0.1	36	11.6 ± 3.0	12.7 ± 3.2	22.3 ± 8.7
1	54	19.6 ± 7.4	25.3 ± 6.2	33.6 ± 11.5
10	71	29.9 ± 7.7	36.1 ± 5.4	51.2 ± 13.4
100	103	46.0 ± 13.9	60.8 ± 12.4	84.5 ± 14.3
Vascular plants				
0.0001	8	1.3 ± 1.1	1.2 ± 0.8	3.8 ± 1.7
0.001	11	1.6 ± 1.5	2.1 ± 1.1	6.2 ± 2.3
0.01	18	2.4 ± 2.4	3.9 ± 2.0	10.6 ± 3.7
0.1	33	7.0 ± 1.9	9.2 ± 2.9	21.6 ± 8.2
1	49	14.7 ± 7.2	18.6 ± 3.8	31.3 ± 11.4
10	66	20.0 ± 4.6	26.9 ± 4.0	46.6 ± 14.8
100	94	30.0 ± 3.6	43.0 ± 8.6	75.7 ± 17.9
Bryophytes				
0.0001	3	0.6 ± 1.1	0.8 ± 1.1	0.2 ± 0.6
0.001	3	1.1 ± 1.3	0.9 ± 1.3	0.3 ± 0.6
0.01	5	1.9 ± 2.0	1.3 ± 1.9	0.5 ± 0.7
0.1	7	3.7 ± 2.5	2.3 ± 2.3	1.1 ± 1.0
1	8	4.0 ± 2.7	3.8 ± 1.9	2.1 ± 1.5
10	14	6.6 ± 3.9	5.6 ± 2.1	3.5 ± 1.9
100	17	10.3 ± 5.9	9.0 ± 2.2	6.2 ± 1.7
Lichens				
0.0001	1	0.1 ± 0.4	0.1 ± 0.3	0.0 ± 0.0
0.001	2	0.3 ± 0.8	0.2 ± 0.4	0.1 ± 0.3
0.01	2	0.6 ± 1.0	0.3 ± 0.5	0.1 ± 0.3
0.1	3	0.9 ± 1.2	1.1 ± 1.3	0.1 ± 0.3
1	9	1.9 ± 2.7	3.0 ± 2.4	0.1 ± 0.4
10	9	3.3 ± 3.7	3.7 ± 2.1	0.6 ± 1.2
100	17	5.7 ± 4.7	8.8 ± 5.6	2.7 ± 5.6

Table 3. Biodiversity, structural and ecological characteristics of all 10 m² plots across the three orders. The *p*-values and significance levels refer to ANOVAs.

Parameter	All (*n* = 67) Mean	Min.	Max.	Order A (*n* = 14) Mean ± SD	Order B (*n* = 15) Mean ± SD	Order C (*n* = 38) Mean ± SD	*p*-value	Significance
Species richness								
Species richness (all taxa)	40.4	18	87	28.8 ± 6.9	34.4 ± 5.6	47.0 ± 15.8	<0.001	***
Species richness (vascular plants)	34.2	16	71	20.9 ± 4.2	26.1 ± 3.7	42.4 ± 14.6	<0.001	***
Species richness (bryophytes + lichens)	6.1	0	23	7.9 ± 7.9	8.3 ± 3.4	4.6 ± 4.1	0.021	*
Species richness (red-listed species)	2.5	0	9	2.9 ± 2.5	3.1 ± 1.5	2.1 ± 1.6	0.109	
Vegetation structure								
Cover vegetation [%]	78	30	100	64 ± 15	58 ± 18	90 ± 15	<0.001	***
Cover herb layer [%]	72	20	100	58 ± 22	47 ± 16	87 ± 18	<0.001	***
Cover bryophyte + lichen layer [%]	13	0	60	14 ± 20	18 ± 20	11 ± 15	0.423	
Cover litter [%]	29	0	95	22 ± 23	21 ± 16	35 ± 28	0.091	
Herb layer height mean [cm]	14.1	1.4	62.6	11.5 ± 9.5	8.4 ± 5.6	17.3 ± 12.5	0.018	*
Herb layer height SD [cm]	6.8	0.8	33.4	8.3 ± 9.0	5.6 ± 6.0	6.7 ± 6.4	0.564	
Ecological indicator values (not weighted by cover)								
EIV light	7.5	6.8	8.1	7.7 ± 0.3	7.8 ± 0.1	7.3 ± 0.2	<0.001	***
EIV temperature	5.4	3.2	6.2	5.8 ± 0.3	5.9 ± 0.1	5.1 ± 0.9	<0.001	***
EIV continentality	4.2	3.5	5.0	4.4 ± 0.3	4.5 ± 0.2	4.1 ± 0.3	<0.001	***
EIV moisture	3.4	2.6	4.9	3.0 ± 0.3	2.8 ± 0.1	3.9 ± 0.6	<0.001	***
EIV reaction	6.9	5.4	8.1	7.3 ± 0.4	6.8 ± 0.4	6.9 ± 0.7	0.031	*
EIV nutrients	2.7	1.6	4.6	2.3 ± 0.7	2.2 ± 0.2	3.1 ± 0.6	<0.001	***
Topography								
Elevation [m]	1180	549	1945	1078 ± 274	1114 ± 120	1243 ± 390	0.191	
Inclination [°]	36	8	59	40 ± 5	38 ± 7	33 ± 10	0.017	*
Southing	0.76	-0.97	1.00	0.79 ± 0.48	0.86 ± 0.31	0.71 ± 0.46	0.518	
Heat index	0.36	-0.98	1.19	0.36 ± 0.48	0.42 ± 0.38	0.34 ± 0.38	0.820	
Maximum microrelief [cm]	15	2	105	20 ± 12	23 ± 25	11 ± 7	0.011	*
Soil parameters [general]								
Cover rocks and stones [%]	18	0	85	37 ± 25	34 ± 28	5 ± 11	<0.001	***
Cover gravel [%]	7	0	50	16 ± 14	8 ± 11	3 ± 10	0.002	**
Cover fine soil [%]	73	1	100	41 ± 34	62 ± 29	89 ± 23	<0.001	***
Soil depth mean [cm]	17	1	56	11 ± 6	9 ± 5	22 ± 15	<0.001	***
Soil depth CV	58	12	225	73 ± 41	89 ± 66	40 ± 21	<0.001	***
Soil parameters [physical]								
Skeleton content [%]	31	0	77	44 ± 18	26 ± 8	28 ± 12	<0.001	***
Sand content [%]	70	48	81	70 ± 7	74 ± 3	68 ± 9	0.036	*
Silt content [%]	14	6	31	14 ± 5	12 ± 3	15 ± 6	0.170	
Clay content [%]	16	11	29	16 ± 4	14 ± 1	17 ± 4	0.060	
Water at saturation [%]	42.7	4.7	48.3	43.3 ± 1.5	42.4 ± 0.6	42.6 ± 6.6	0.863	
Water at field capacity [%]	20.5	17.9	27.7	20.5 ± 1.9	19.3 ± 0.7	21.1 ± 2.5	0.028	*
Water at permanent wilting point [%]	11.3	9.4	16.7	11.3 ± 1.5	10.5 ± 0.5	11.6 ± 1.8	0.063	
Plant-available water [%]	9.2	8.1	12.2	9.2 ± 0.7	8.8 ± 0.4	9.4 ± 1.0	0.080	
Drainage rate [cm/h]	1.3	0.3	2.2	1.3 ± 0.5	1.6 ± 0.3	1.2 ± 0.5	0.053	
Soil parameters [chemical]								
pH [in aqua dest.]	6.87	4.34	8.34	7.37 ± 0.56	6.87 ± 0.55	6.67 ± 1.02	0.040	*
Electrical conductivity [µS/cm]	148	25	511	214 ± 138	90 ± 53	147 ± 110	0.011	*
Organic matter [%]	14.2	6.0	32.3	16.4 ± 7.5	11.8 ± 5.1	14.4 ± 7.2	0.209	
Organic carbon [%]	8.2	3.5	18.8	9.5 ± 4.3	6.8 ± 3.0	8.3 ± 4.2	0.212	
N content [%]	1.4	0.1	4.6	2.0 ± 0.9	1.0 ± 0.6	1.4 ± 0.8	0.004	**
C/N ratio	7.9	2.8	61.8	4.8 ± 1.7	9.0 ± 6.8	8.6 ± 10.6	0.326	
P available [ppm]	18.5	8.8	47.3	23.1 ± 12.6	17.5 ± 5.0	17.2 ± 8.9	0.120	

sizes, maximum species richness was much higher for vascular plants (e.g. 94 species in 100 m²) compared to bryophytes and lichens (e.g. 17 species each in 100 m²) (Table 2). When comparing the mean species richness of vascular plants across the three orders, for all taxa as well as for vascular plants alone, order C was by far the richest, while order B was intermediate and order A poorest (Tables 2 and 3). For example, mean total richness in 10 m² decreased from 51.2 in order C via 36.1 in order B to 29.9 in order A. By contrast, bryophytes and lichens across all grain sizes were always richer in orders A and B than in order C, with little difference between the former (Tables 2 and 3). At the association level, the richness patterns were more diverse (Table 4, Figure 6): While species richness of vascular plants in all associations of orders A (rocky) and B (xeric) were equally low (around 20 in 10 m²), in order C (meso-xeric) they ranged from 27 in C.1 to 54 in C.5. Mean richness of non-vascular taxa in 10 m² varied strongly within the orders, ranging from 0.3 to 16.6 in order A and from 1.3 to 9.6 in order C. Herb layer cover was generally higher in the meso-xeric communities (order C) compared to the xeric and rocky ones (orders A and B) (Tables 3 and 4, Figure 6), while cover values of non-vascular taxa varied independently of the order and were largely consistent with the respective richness patterns (Figure 6).

While we found the highest mean species richness of vascular plants in the mountain meadows of C.5

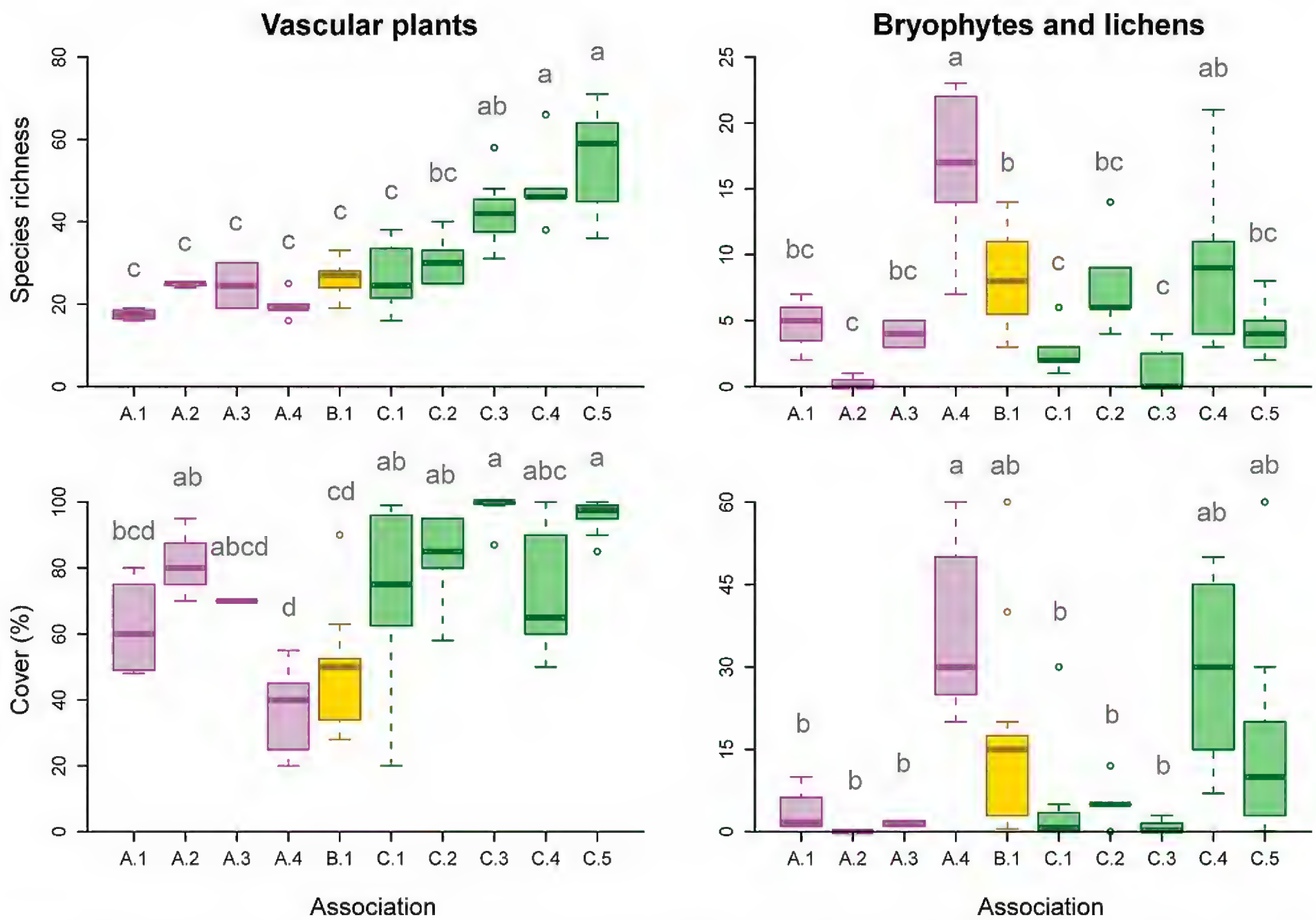


Figure 6. Comparison of species richness and cover of the two taxonomic-functional groups among the plots of the 10 communities at association rank. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

(58.5 species in 10 m²), the record (87 species on 10 m²) occurred in a plot of C.4 with shallow, acidic soil, grazed by cattle, sheep and goats in Fließ (Suppl. material 1). The highest cryptogam species richness was in a stand of A.4, a historically and recently grazed hill on calcareous slate in the Virgen valley in East Tyrol (Suppl. material 1). Concerning red list species, the non-managed steep grasslands on serpentinite (cluster A.1) had the highest values (Suppl. material 1), as many of the species are edaphic specialists with a restricted distribution.

Site conditions

According to all ecological indicator values except soil reaction, orders A and B were indistinguishable, but different from the meso-xeric order C, whose species composition stands for less light, lower temperature, lower continentality, more moisture and more nutrients (Table 3, Figure 7). By contrast, EIVs for soil reaction were high in order A, low in order B and intermediate in order C (Table 3, Figure 7). In general, measured topographic and soil variables showed only weak or no systematic difference between the orders, except skeleton content, which was clearly higher in the rocky grassland order A (Table 3).

At the association level, there were also strong differences for most of the measured variables (Table 4), with the most prominent ones shown in Figure 8: Within both the rocky and the meso-xeric order, the associations were segregated along an elevation gradient, with A.1 and C.3 occurring at the lowest and A.4 and C.5 at the highest elevations. Rock and stone cover generally was higher and more variable in the associations of the rocky and xeric orders (except A.3) compared to the meso-xeric associations. Soil depth in most communities was low (around 10–15 cm), but much higher in C.3 and C.5 (around 30 cm). Soil pH was high in most of the associations (6.9–7.4), but lower in C.4 (6.3) and much lower in C.2 (4.7). Nutrient concentrations (N and P) were generally low, with the noticeable exception of association A.2 with approximately two times higher values than all other associations.

Description of the associations and communities

In the following paragraphs, the ten accepted vegetation units at association level are described, and their syntaxonomic position is discussed. Four units could be unambiguously assigned to described associations, while the six remaining ones are labelled with informal community names.

Table 4. Biodiversity, structural and ecological characteristics across the 10 association-level communities. The *p*-values and significance levels refer to ANOVAs.

Parameter	A.1 (*n* = 4)	A.2 (*n* = 3)	A.3 (*n* = 2)	A.4 (*n* = 5)	B.1 (*n* = 15)	C.1 (*n* = 8)	C.2 (*n* = 5)	C.3 (*n* = 7)	C.4 (*n* = 5)	C.5 (*n* = 13)	*p*-value	
Species richness												
Species richness (all taxa)	22.3	25.0	28.5	36.4	34.4	29.3	38.4	43.7	58.4	58.5	<0.001	***
Species richness (vascular plants)	17.5	24.7	24.5	19.8	26.1	26.6	30.6	42.4	48.8	54.1	<0.001	***
Species richness (bryophytes + lichens)	4.8	0.3	4.0	16.6	8.3	2.6	7.8	1.3	9.6	4.5	<0.001	***
Species richness (red-listed species)	6.0	2.7	2.0	1.0	3.1	3.1	3.2	2.1	1.2	1.2	<0.001	***
Vegetation structure												
Cover vegetation [%]	63	82	70	53	58	76	86	98	88	98	<0.001	***
Cover herb layer [%]	62	82	70	37	47	73	83	98	73	96	<0.001	***
Cover bryophyte + lichen layer [%]	4	0	2	37	18	5	5	1	29	15	0.001	***
Cover litter [%]	8	43	55	8	21	48	40	56	19	20	<0.001	***
Herb layer height mean [cm]	13.9	16.7	10.3	7.0	8.4	10.4	22.8	32.6	11.9	13.4	<0.001	***
Herb layer height SD [cm]	12.0	7.2	6.1	7.0	5.6	3.3	17.4	9.5	4.0	4.1	0.008	**
Ecological indicator values												
EIV light	7.7	7.5	7.5	8.0	7.8	7.5	7.3	7.1	7.1	7.3	<0.001	***
EIV temperature	6.0	6.0	6.0	5.5	5.9	5.8	5.7	5.6	5.2	4.0	<0.001	***
EIV continentality	4.6	4.6	4.2	4.2	4.5	4.5	4.0	4.2	3.6	3.9	<0.001	***
EIV moisture	2.9	3.2	3.4	2.8	2.8	3.1	3.6	3.8	4.2	4.3	<0.001	***
EIV reaction	7.3	7.6	7.7	7.1	6.8	7.6	5.8	7.4	6.3	6.8	<0.001	***
EIV nutrients	2.0	3.1	3.3	1.8	2.2	2.6	2.9	3.7	3.4	3.0	<0.001	***
Topography												
Elevation [m]	810	899	1055	1410	1114	1112	905	854	1212	1675	<0.001	***
Inclination [°]	45	41	35	38	38	36	22	38	30	33	0.010	**
Southing	0.49	0.94	0.98	0.87	0.86	0.95	0.89	0.92	0.16	0.62	0.031	*
Heat index	0.32	0.40	0.40	0.35	0.42	0.45	0.20	0.71	0.16	0.21	0.322	
Maximum microrelief [cm]	30	11	26	15	23	11	15	8	17	7	0.083	
Soil parameters [general]												
Cover rocks and stones [%]	41	22	8	54	34	9	11	1	9	0	<0.001	***
Cover gravel [%]	18	10	25	15	8	3	1	7	8	0	0.047	*
Cover fine soil [%]	24	68	68	29	62	77	88	92	83	99	<0.001	***
Soil depth mean [cm]	9	18	13	6	9	14	8	33	11	31	<0.001	***
Soil depth CV	79	46	95	77	89	37	54	29	45	40	0.019	*
Soil parameters [physical]												
Skeleton content [%]	53	52	37	36	26	26	30	26	22	31	0.002	**
Sand content [%]	67	70	74	71	74	75	62	67	61	70	0.004	**
Silt content [%]	14	15	10	15	12	10	22	16	20	14	0.002	**
Clay content [%]	18	16	16	14	14	15	16	18	20	16	0.182	
Water at saturation [%]	44.3	43.3	43.2	42.6	42.4	42.8	44.0	44.0	45.0	39.9	0.739	
Water at field capacity [%]	21.6	20.4	20.1	19.8	19.3	19.7	21.7	21.5	23.0	20.7	0.037	*
Water at permanent wilting point [%]	12.3	11.2	11.4	10.5	10.5	11.1	11.3	12.0	12.8	11.5	0.178	
Plant-available water [%]	9.4	9.3	8.7	9.3	8.8	8.6	10.4	9.5	10.2	9.2	0.002	**
Drainage rate [cm/h]	1.0	1.3	1.3	1.6	1.6	1.4	1.3	1.1	1.0	1.3	0.192	
Soil parameters [chemical]												
pH [in aqua dest.]	7.12	7.27	7.35	7.64	6.87	7.22	4.73	7.15	6.28	7.00	<0.001	***
Electrical conductivity [µS/cm]	275	263	112	175	90	84	77	203	193	167	0.010	**
Organic matter [%]	19.9	25.7	11.3	10.0	11.8	12.7	25.8	13.6	15.0	11.0	<0.001	***
Organic carbon [%]	11.5	14.8	6.5	5.8	6.8	7.3	14.9	7.9	8.6	6.3	<0.001	***
N content [%]	1.7	3.3	1.6	1.7	1.0	0.9	2.1	1.4	2.1	1.2	<0.001	***
C/N ratio	7.0	4.4	4.1	3.6	9.0	14.1	8.2	5.7	4.6	8.4	0.589	
P available [ppm]	17.1	38.5	29.8	16.0	17.5	14.6	28.2	21.6	15.5	12.7	<0.001	***

A.1 *Armerio elongatae-Potentilletum arenariae*
(relevés 1–4 in Suppl. material 2, Table 1, Figure 9a)

Characterisation: Rocky grasslands on serpentine bedrock with low vegetation cover (48–80%). They are dominated by *Festuca pallens* and *Potentilla incana* with *Carex humilis*, *Dorycnium germanicum* and *Thymus praecox* as occasional subdominants. Among the species diagnostic or constant for this association, *Asplenium cuneifolium*, *Erysimum sylvestre*, *Koeleria pyramidata* var. *pubiculmis*, *Notholaena marantae* and *Silene otites* were recorded in our relevés. The cryptogam layer covered 1% to 10% of the surface and was dominated by *Rhytidium rugosum* and *Weissia brachycarpa*. The latter species, together with *Fissidens dubius* and *Mannia fragrans*, belongs to the diagnostic species of the association in our data set.

Ecology and distribution: Our relevés were recorded on very steep slopes with predominantly southern aspect and elevation between 785 and 830 m. The rugged terrain had a high cover of rocks and gravel on the surface and very shallow soils rich in skeleton. The high soil pH is typical for serpentinite (in this case it corresponds quite well with mean EIV-R of 7.2). N and P are rather low, but organic matter is high, even if there is a strikingly low litter cover (Table 4). Most of these species are adapted to the high magnesium soil content of the serpentine habitats. There is no management on these steep and dry southern slopes, although there is some moderate grazing by

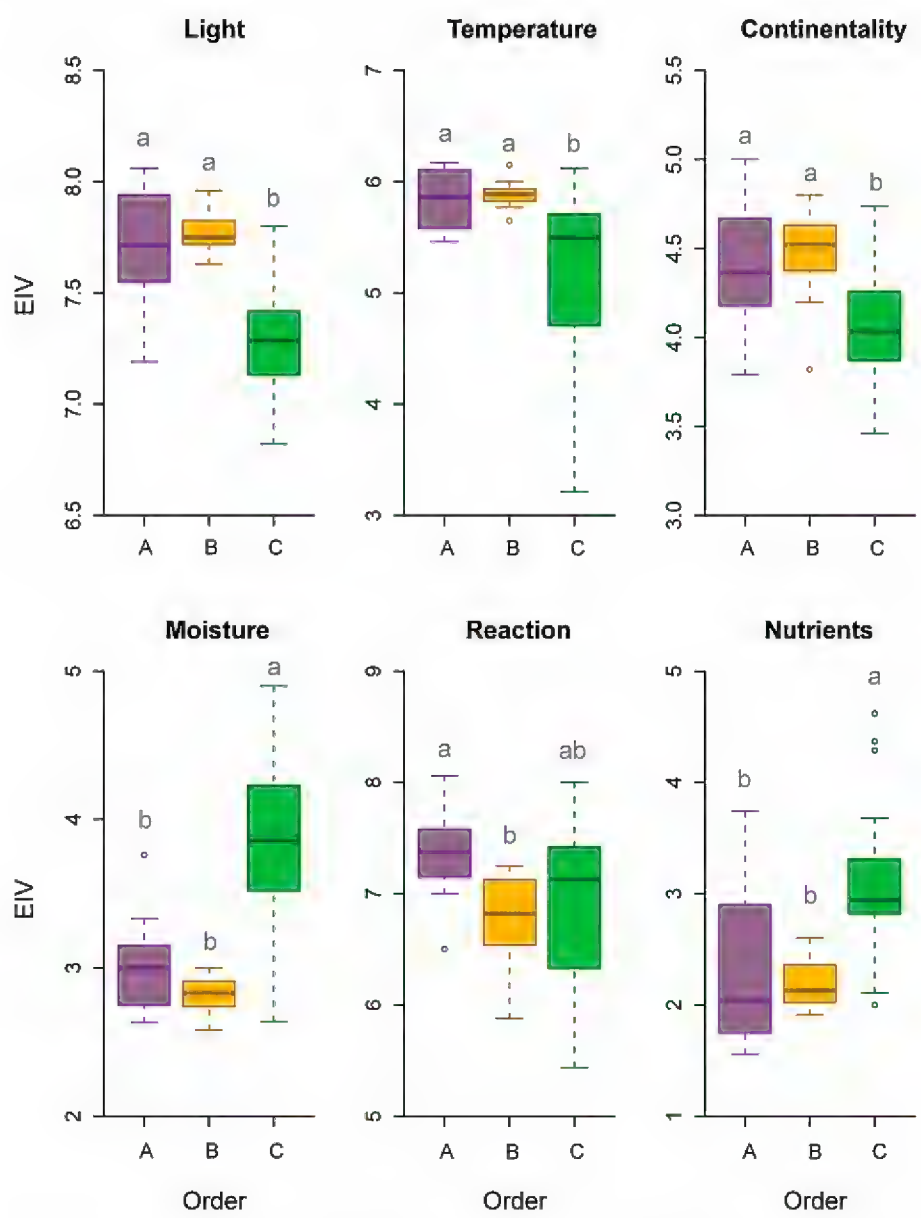


Figure 7. Comparison of six mean ecological indicator values among the plots of the three orders A (*Stipo-Festucetalia pallentis*), B (*Festucetalia valesiacae*) and C (*Brachypodietalia pinnati*). Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

Rupicapra. Nevertheless, there is no litter accumulation, and the low productivity seems in balance with the humification, as shown by the high organic matter content. In this cluster, we found the highest number and cover of red-list species, although the total species number was low. The special weathering of the serpentinite, which leads to very steep slopes, the dark soil surface caused by the high organic content, the low soil depth, the high soil magnesium content, and the position at a narrow section of the valley that increases wind velocity, interact to a very dry and specific habitat type. The history of this habitat might date back to the Neogene, as indicated by the occurrence of the palaeoendemic *Sempervivum pittonii* (Magnes et al. 2020), which has its closest relative in Bulgaria (Lippert 1995). The association is probably endemic to Styria, besides Gulsen occurring also near Kirchdorf und Traföß ("Tragöß") about 30 km downstream the Mur river where the serpentine layer reaches the surface again (Mucina and Kolbek 1993).

Syntaxonomy: Our relevés are from the locus classicus of this association, which was described by Braun-Blanquet (1961) and included in the alliance *Stipo-Poion xerophilae* and in the order *Festucetalia valesiacae*. Mucina and Kolbek (1993) described a new alliance *Avenulo adsurgentis-Festucion pallentis* within the *Stipo-Festucetalia pallentis*, based on the *Armerio-Potentilletum* as holotype. This alliance was intended to include all dry grasslands on serpentine in Austria. However, the alliance name is invalidly published as the name-giving *Avenula adsurgens* is not present in the original diagnosis (Art. 3f ICPN, Theurillat et al. 2021).

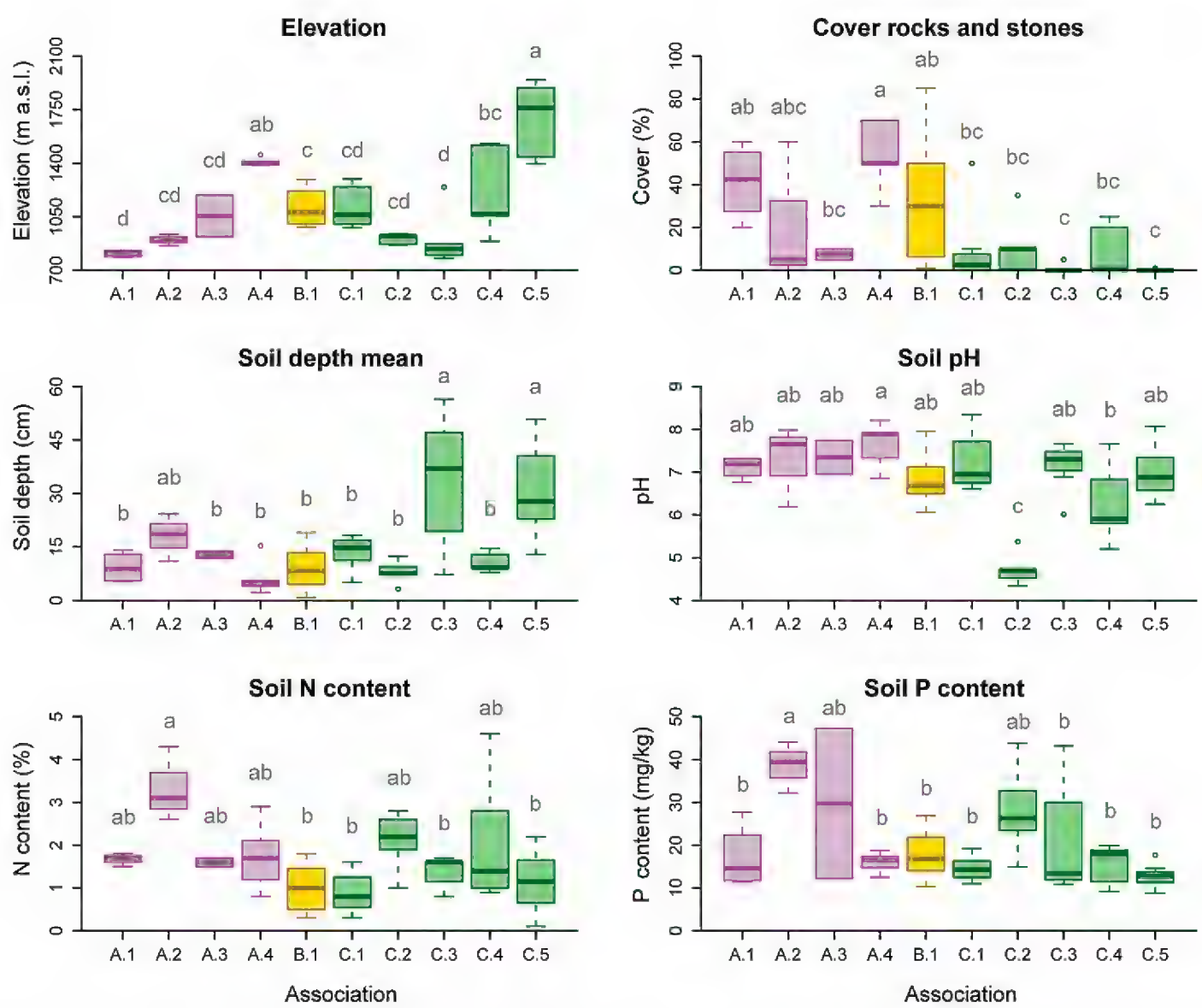


Figure 8. Comparison of six measured ecological variables among the plots of the 10 communities at association rank. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

A.2 *Phleo phleoidis-Pulsatilletum nigricantis*

(relevés 5–7 in Suppl. material 2, Table 1, Figure 9b–d)

Characterisation: Rocky grasslands on steep, south-facing slopes at elevations between 861 and 935 m. The vegetation is almost closed with bryophyte and lichen layers nearly absent (Table 4). The community is dominated by *Carex humilis* and *Festuca rupicola* with a constant occurrence of *Allium lusitanicum*, *Fallopia convolvulus*, *Origanum vulgare*, *Stachys recta*, *Teucrium chamaedrys*, and *Verbascum chaixii* subsp. *austriacum*. The endangered *Stipa styriaca* reached its highest cover in this association.

Ecology and distribution: The sampled stands were not managed. They have deep soils, the second highest organic matter content among all clusters and also relatively high litter cover, P and N (Table 4). The plots show clear indication of grassland abandonment. Apart from Pöls (PÖ) we recorded this vegetation around the Puxer Loch (PU), a medieval cave castle in a Paleozoic lime cliff, where *Galium mollugo* agg. was dominant.

Syntaxonomy: This unit perfectly matches the association *Phleo-Pulsatilletum nigricantis* described by Braun-Blanquet (1961) from various locations in Carinthia and one location in Styria. As in the previous unit, Braun-Blanquet included this association in the alliance *Stipo-Poion xerophilae*. Following a proposal by Franz (1988), Mucina and Kolbek (1993) merged the *Phleo-Pulsatilletum nigricantis* with the *Potentillo puberulae-Festucetum sulcatae* Br.-Bl. 1961 and transferred it to the alliance *Festucion valesiacae*. However, while the *Potentillo puberulae-Festucetum sulcatae* has indeed a strong affinity to the *Festucion valesiacae*, the *Phleo-Pulsatilletum nigricantis* clearly belongs to the *Stipo-Festucetalia pallentis*. We therefore suggest maintaining the *Phleo-Pulsatilletum nigricantis* as a separate association, which probably includes all rocky grasslands on relatively well-developed soils in the Styrian and Carinthian part of the Austrian central Alps. As in other regions of Central Europe, these moderate rocky grasslands have a more or less closed herb layer and are dominated by *Carex humilis* and *Festuca rupicola* (Janišová and Dúbravková 2010; Willner et al. 2013). The exact delimitation towards the *Seselietum austriacae* Br.-Bl. 1961, which comprises the more extreme, open rocky grasslands with *Festuca pallens* in the same region, requires further studies.

A.3 *Medicago minima-Melica ciliata* community

(relevés 8–9 in Suppl. material 2, Table 1, Figure 9e)

Characterisation: Cluster A.3 only includes two relevés from the Upper Inn valley, dominated by *Melica ciliata*. The vegetation cover is 70% while the cryptogam layer is poorly developed, covering only below 2%. Along with *Melica ciliata*, some other species have a high cover, such as *Artemisia absinthium*, *Brachypodium pinnatum*, *Bromus erectus*, *Galium lucidum* and *Thymus praecox*. Less abundant are *Agrimonia eupatoria*, *Carex humilis* and *Medicago minima*.

Ecology and distribution: The shallow soils on the steep south-facing upper slopes show a high skeleton content, high pH and P, but low N and organic matter, although the litter cover is very high (Table 4). Both sites were not managed. One is overgrown by shrubs (*Berberis vulgaris*, *Euonymus europaeus*, *Prunus spinosa*), and the other one has a strongly developed litter layer covering 80% of the soil surface. The number of species is low in all categories. We recorded this community in the Upper Inn valley, in FL and LA.

Syntaxonomy: This unit does not match any described association from the Eastern Alps. The closest syntaxon from the literature is the *Astragalo-Brometum stipetosum capillatae* of Kielhauser (1954), which was raised to association rank by Mucina and Kolbek (1993) under the name *Achnathero-Stipetum capillatae*.

A.4 *Koelerio pyramidatae-Teucrietum montani*

(relevés 10–14 in Suppl. material 2, Table 1, Figure 9f)

Characterisation: Rocky grasslands on extremely shallow soils on calcareous slate (Table 4). The most constant and abundant species in the herb layer are *Festuca rupicola*, *Koeleria pyramidata* and *Potentilla pusilla*. Further, *Allium lusitanicum*, *Artemisia campestris*, *Dianthus sylvestris*, *Juniperus sabina*, *Sedum album*, *Sempervivum wulfenii* and *Teucrium montanum* were constantly present. The most important diagnostic species are *Poa badensis* agg., *Saxifraga paniculata*, the lichens *Peltigera rufescens* and *Toninia sedifolia* as well as the bryophytes *Tortella inclinata* and *T. tortuosa*. Numerous further lichen species show high constancy and fidelity to this plant community, e.g. *Buellia elegans*, *Cladonia symphycarpa*, *C. pyxidata*, *Endocarpon pusillum*, *Physconia muscigena* and *Psora decipiens*. The most frequent bryophytes are *Abietinella abietina*, *Ditrichum flexicaule* and *Tortella inclinata*.

Ecology and distribution: Most of the surface (30–90%) is covered by rocks or gravel. Litter cover and organic content are low, like N and P content, with a high pH (Table 4). The plant layer is open, covering between 40 and 60%, and it is quite species poor, containing only 16 to 19 vascular plant species in 10 m^2. The cryptogam layer is well-developed, covering between 40 and 60% of the soil surface, and rich in species (median species number is 17, maximum 23 including both bryophytes and lichens), being the highest values of all clusters. In the past (until several decades ago) most of these grasslands were grazed by sheep. The lichen *Thamnolia vermicularis* subsp. *subuliformis*, which has its preferred habitat on alpine wind-heathland on stony open soil (Wirth et al. 2013; Nimis et al. 2018), is a witness for transport of thallus fragments by sheep because this wormlike fruticose chalk-white lichen never develops vegetative propagules such as isidia or soredia. Recently, all of these grasslands have been moderately grazed by cattle. We recorded the association in Obermauern (OM) in the Virgen valley (East Tyrol) on the top and southern and southeastern slopes of a hill called "Burg", at elevations of about 1,400 m.

Syntaxomy: This unit corresponds to the association *Koelerio pyramidatae-Teucrietum montani*, first proposed by Franz (1988) and validly described in Mucina and

Figure 9. Photos of associations and communities I. **a.** A.1 *Armerio elongatae-Potentilletum arenariae*, site GU; **b.** A.2 *Phleo-Pulsatilletum nigricantis*, PÖ; **c.** A.2 *Phleo-Pulsatilletum nigricantis*, PÖ; **d.** A.2 *Phleo-Pulsatilletum nigricantis*, PU; **e.** A.3 *Medicago minima-Melica ciliata* community, LA; **f.** A.4 *Koelerio pyramidatae-Teucrietum montani*, OM. Photos: J. Dengler (**a, b, e, f**) and M. Magnes (**c, d**).

Kolbek (1993). While Franz (l.c.) originally placed the association in the *Festucion valesiacae*, the latter authors classified it in the alliance "*Diantho lumnitzeri-Seslerion albicantis*". The community has some similarity with the *Teucrio-Caricetum humilis* Br.-Bl. 1961, which is traditionally classified in the *Stipo-Poion xerophilae* and includes rocky grasslands in the Upper Inn valley (Braun-Blanquet 1961; Mucina and Kolbek 1993). However, according to the species list in Franz (1988) and our own relevés, *Carex humilis* seems to be absent in this association. The floristic

relationship between *Teucrio-Caricetum humilis* and *Koelerio-Teucrietum montani* should be further addressed in future studies.

B.1 *Sempervivum tectorum-Festuca valesiaca* community

(relevés 15–29 in Suppl. material 2, Table 1, Figure 10a)

Characterisation: This unit was documented from the Upper Inn valley, between 983–1,295 m on steep slopes. The rather low litter cover is connected with a high number and cover of cryptogams, indicated by the saxicole species *Grimmia ovalis*, *G. laevigata* and *Hedwigia ciliata* occurring on the rocks and *Crossidium squamiferum* and *Tortula ruralis* as bryophytes from open dry soil, interwoven by the common pleurocarpous dry grassland species *Abietinella abietina* and *Rhytidium rugosum*. Among grasses, *Festuca valesiaca* has a high constancy and cover. A fairly high number of annual species, typical of *Sedo-Scleranthetea*, form the largest bulk of diagnostic species.

Ecology and distribution: Shallow soils with rather low litter cover and organic content, and low N and P (Table 4). The community was recorded only in the Upper Inn valley (KA, FL and LA).

Syntaxonomy: This cluster is transitional between the orders *Stipo-Festucetalia pallentis* and *Festucetalia valesiacae*. In five relevés, the diagnostic species of the first order are more abundant, in seven relevés those of the second order, while in three relevés both species groups have more or less the same total cover (Figure 4). Diagnostic species of the order *Festucetalia valesiacae* that are present in this unit are *Bothriochloa ischaemum*, *Festuca valesiaca*, *Medicago minima*, *Stipa capillata* and *Trifolium arvense*. Kielhauser (1954) included similar grasslands of the same region in the *Astragalo-Brometum*. However, since the *Astragalo-Brometum* is a *Brachypodietalia* community (see below), this association name cannot be applied to unit B.1. Here, we provisionally include this unit in the alliance *Festucion valesiacae*. Without a comprehensive revision of all inner-alpine dry grasslands it is impossible to say if it might be assigned to one of the numerous associations described by Braun-Blanquet (1961) from South Tyrol and Switzerland, or if it must be described as a new association.

C.1 *Astragalo onobrychidis-Brometum erecti*

(relevés 30–37 in Suppl. material 2, Figure 10b)

Characterisation: Grasslands in the Upper Inn valley dominated by *Bromus erectus* and/or *Brachypodium rupestre*, *Carex humilis* and *Festuca rupicola*. This unit is similar to the previous one, but it has a much lower cover of stones and deeper soils. *Festuca valesiaca*, *Sempervivum tectorum* and other diagnostic species of unit B.1 are rare or absent.

Ecology and distribution: Our plots have open and shallow soils, which are poor in skeleton, organic matter, N and P, with a rather high litter cover (Table 4). Braun-Blanquet (1961) considered the association as typical for the calcareous Bündner schist of the geological unit "Lower Engadine Window", from Ardez in Switzerland to Landeck in Austria.

Syntaxonomy: This cluster can be assigned to the *Astragalo-Brometum*, described from the Lower Engadine (Switzerland) by Braun-Blanquet (1949) and originally included in the *Stipo-Poion xerophilae*. Braun-Blanquet's alliance assignment was followed by Mucina and Kolbek (1993). However, the type relevé of the association (selected by Terzi et al. 2017) clearly belongs to the *Brachypodietalia pinnati*. Likewise, the *Brachypodietalia* species prevail in most relevés of this cluster, although the *Stipo-Festucetalia pallentis* species also have a high proportion (Figure 4). We therefore follow the interpretation of Willner et al. (2019) who included the *Astragalo-Brometum* in the *Cirsio-Brachypodion*. Relevé 49, which contains almost no *Brachypodietalia* species, is probably misclassified. Kielhauser (1954), who studied the dry grasslands in the Tyrolian Upper Inn Valley, distinguished two subassociations within the *Astragalo-Brometum*: the *A.-B. stipetosum capillatae* on steep, rocky slopes (see unit A.3), and the *A.-B. festucetosum valesiacae* on less rocky or even deep soils. However, the latter subassociation is a heterogeneous unit, including both xeric grasslands of the *Festucetalia valesiacae* (corresponding to our unit B.1) and meso-xeric (semi-dry) grasslands of the *Brachypodietalia* (corresponding to the *Astragalo-Brometum* s.str. and our unit C.1).

C.2 *Agrostis capillaris-Avenula adsurgens* community

(relevés 38–42 in Suppl. material 2, Table 1, Figure 10c)

Characterisation: This is a semi-dry grassland with dominant *Agrostis capillaris* and *Koeleria pyramidata* and the presence of several acidophytes like *Avenella flexuosa*, *Potentilla argentea* or *Trifolium arvense*. Remarkable is the occurrence of some very rare lichens like *Rinodina cana* and *R. vezdae* (= *R. moziana*, new for Styria!).

Ecology and distribution: This unit occurs on siliceous soils (significantly lowest pH of all clusters, Table 4) over quartzite bedrock north of Neumarkt in der Steiermark (NM). Litter cover and organic matter are high (the latter is the highest of all clusters, Table 4), a consequence of abandonment as the grassland management was readopted just the year previous to our sampling, and also the high P and N contents are indicative for accumulation processes. The bryophytes *Bryum argenteum* and *Ceratodon purpureus* indicate high nutrient levels.

Syntaxonomy: This community has some similarity with the associations *Chamaecytiso hirsuti-Koelerietum* and *Genisto sagittalis-Festucetum rupicolae*, both (invalidly) described from southern Styria – near to the Slovenian border – by Steinbuch (1995). In the revision of the semi-dry grasslands of Central and Eastern Europe by Willner et al. (2019), the *Chamaecytiso hirsuti-Koelerietum* was partly assigned to the *Festuco rupicolae-Brometum* Zielonkowski 1973, and partly to the *Colchico-Festucetum rupicolae* Lengyel et al. 2016 while the *Genisto-Festucetum rupicolae* remained unclassified, indicating that there are still some unresolved problems in the classification of semi-dry grasslands in Austria. There is also a slight similarity to the *Brachypodio-Avenuletum adsurgentis* that was (also invalidly) described from the Köszeg Mts. in western

Figure 10. Photos of associations and communities II. **a.** B.1 *Sempervivum tectorum-Festuca valesiaca* community, site FL; **b.** C.1 *Astragalo onobrychidis-Brometum erecti*, KA; **c.** C.2 *Agrostis capillaris-Avenula adsurgens* community, NM; **d.** C.3 *Anthericum ramosum-Brachypodium pinnatum* community, PÖ; **e.** C.4 *Ranunculus bulbosus-Festuca rubra* community, MA; **f.** C.5 *Carduus defloratus-Brachypodium pinnatum* community, ZS. Photos: J. Dengler.

Hungary (Kovács 1994). Here, we prefer to use an informal community name for this cluster, leaving the clarification of its syntaxonomic status to a future revision.

C.3 *Anthericum ramosum-Brachypodium pinnatum* community

(relevés 43–49 in Suppl. material 2, Table 1, Figure 10d)

Characterisation: These semi-dry grasslands on calcareous soils are dominated by *Brachypodium pinnatum* and *Festuca rupicola*. *Clinopodium vulgare*, *Salvia pratensis*, *Vincetoxicum hirundinaria*, *Viola hirta*, and together with *Molinio-Arrhenatheretea* taxa such as *Achillea millefolium* agg., *Arrhenatherum elatius*, *Dactylis glomerata*, *Taraxacum* sect. *Ruderalia* and *Tragopogon orientalis* are also common.

Ecology and distribution: This cluster mainly includes the semi-dry grasslands on base rich, very deep and fine soils near Pöls (PÖ) that had been abandoned for years before grassland management was started again by clearing shrubs only a few years ago. Because of the occurrence of *Stipa styriaca*, the site was declared as a Natura 2000 protected area. With the reintroduction of

grazing by sheep in 2020, there is a good chance that *Stipa* will be able to spread again from the rocky areas (see unit A.2) to the parts with deep soils. In this community, there is nearly no rock and gravel cover and also skeleton soil content, P and N are low (Table 4). The high litter cover does not lead to high organic matter, but suppresses the development of a bryophyte layer as well as the germination of most vascular plant species. The one relevé from Griffen (variant a) represents a grassland parcel within the bounding walls of the castle that was cleared from trees a few years ago, and the grassland management was started only after that. One relevé from Tyrol (KA) is included in this cluster as well.

Syntaxonomy: Three geographical variants can be distinguished in this cluster: The relevé from Griffen (variant a) is a strongly disturbed, ruderalized grassland of doubtful phytosociological position. The relevé from Kaunerberg (variant c) might represent a more mesic variant of the *Astragalo-Brometum* (see unit C.1). The remaining relevés (variant b) could be assigned to the *Scabioso ochroleucae-Brachypodietum* Klika 1933, which was described in Bohemia (Klika 1933). This association has not been reported from Austria before, but its presence in the Eastern Alps was predicted by the expert system developed by Willner et al. (2019). Against its Pannonian vicariant *Polygalo majoris-Brachypodietum* Wagner 1941, the *Scabioso ochroleucae-Brachypodietum* is only negatively differentiated.

C.4 *Ranunculus bulbosus-Festuca rubra* community

(relevés 50–54 in Suppl. material 2, Table 1, Figure 10e)

Characterisation: This unit lacks dominant species, but some *Molinio-Arrhenatheretea* species show high constancy, like *Achillea millefolium* agg., *Festuca rubra* agg., *Plantago lanceolata* and *Trifolium pratense*. Species number is very high, especially in variant (b) from FL, as well as cryptogam species number and cover.

Ecology and distribution: The soils are shallow and pH is remarkably low (with the exception of variant c) and both litter cover and organic soil matter are low (Table 4). P is low, while N has high values, especially in variant (b). The bryophyte layer with *Calliergonella cuspidata*, *Plagiomnium undulatum* and *Thuidium philibertii* shows a good water supply. The cluster includes relevés from three locations from each of the investigated main valley systems (NM, MA, FL).

Syntaxonomy: This is a rather heterogeneous cluster consisting of three geographical variants. Variant (a) includes a single relevé from Neumarkt in der Steiermark (NM), which is dominated by *Arrhenatherum elatius* and might belong to the alliance *Arrhenatherion* (class *Molinio-Arrhenatheretea*). Variant (b) contains two relevés from the Upper Inn Valley (FL), which have a high portion of acidophilous species (e.g. *Calluna vulgaris*, *Danthonia decumbens*, *Viola canina*). These relevés have some similarity with the *Agrostio-Dianthetum deltoidis*, which was described by Braun-Blanquet (1976) in the Lower Engadin and the Val Müstair (Switzerland). Variant (c) comprises two relevés from Virgen (MA) that share some species with the next unit.

C.5 *Carduus defloratus-Brachypodium pinnatum* community

(relevés 55–67 in Suppl. material 2, Table 1, Figure 10f)

Characterisation: Semi-dry grasslands in the montane and subalpine belt on steep southern slopes dominated by *Brachypodium pinnatum* agg. and *Laserpitium latifolium* and with (sub)alpine species such as *Astragalus penduliflorus*, *Campanula scheuchzeri*, *Carex sempervirens*, *Festuca norica*, *Plantago atrata*, *Rhinanthus glacialis* and *Soldanella alpina*.

Ecology and distribution: Grasslands on deep soils with low organic matter and low P and N (Table 4), mainly found in the Virgen valley. The subalpine plots from ZS and FL represent subalpine hay-meadows. The montane grassland in MA was managed similarly, mown only once and late in the year (August) without any fertilization. Although the subalpine grassland from ZS, an avalanche corridor, is not mown anymore, litter cover is low in all plots. Together with cluster 10b (part of C.4) we found here the highest vascular species number.

Syntaxonomy: This community is characterised by the presence of several subalpine and alpine species and therefore is transitional towards the class *Elyno-Seslerietea*. In this respect, it is similar to the *Carlino-Caricetum sempervirentis* Lutz et Paul 1947 of the northern Alps. According to the alliance concept of Willner et al. (2019), the *Carlino-Caricetum sempervirentis* belongs to the *Mesobromion*, while the grasslands in East Tyrol probably belong to the *Cirsio-Brachypodion*. However, the diagnostic species of the latter alliance are not very abundant in this cluster, and in some relevés they are even completely absent. Thus, the alliance assignment remains provisional. Another association that has similarity with this cluster is the *Centaureo-Gentianetum cruciatae*, described by Braun-Blanquet (1976) from the Upper and Lower Engadine (Switzerland). Some relevés from the highest elevations might already belong to the *Campanulo scheuchzeri-Festucetum noricae* Isda 1986 (alliance *Caricion ferruginei*, see Grabherr et al. 1993), that was mentioned from other alpine hay meadows in the Virgen valley (Isda 1986).

Discussion

Alliances and orders

While the assignment of the TWINSPAN clusters to phytosociological orders was relatively straightforward, the identification of the alliances remains doubtful for the most part.

The rocky grasslands of the Eastern Alps were included in three alliances by Mucina and Kolbek (1993): *Avenulo adsurgentis-Festucion pallentis* (comprising the *Armerio elongatae-Potentilletum arenariae* as the only association),

Diantho-Seslerion (comprising the rocky grasslands on calcareous soils from East Tyrol and Salzburg eastwards) and *Stipo-Poion xerophilae* (comprising all dry grassland of the Inn valley). However, none of these names is acceptable because (1) the *Avenulo adsurgentis-Festucion pallentis* is not validly published (see description of unit A.1), (2) the *Diantho-Seslerion* is based on associations of the Bükk mountains in Hungary that are very different from the rocky grasslands of the Alps (see remark in the syntaxonomic scheme below), and (3) the *Stipo-Poion xerophilae* has been typified with a *Festucetalia valesiacae* community of the Vinschgau (Terzi et al. 2017). Thus, it seems that the rocky grasslands of the Eastern Alps are lacking a valid alliance name, unless they are included in a broadly conceived *Seslerio-Festucion pallentis* Klika 1931. However, it is impossible to decide from our dataset whether all rocky grasslands belong to the same alliance, or if they can be included in one of the alliances described from the Pannonian Basin. Therefore, we refrain from assigning our *Stipo-Festucetalia pallentis* communities to an alliance and leave this question to a broad-scale syntaxonomic revision of the order.

Grass steppes of the *Festucetalia valesiacae* are represented by a single community in our data set (*Sempervivum tectorum-Festuca valesiaca* community), which probably can be assigned to the *Festucion valesiacae*. It must be noted, however, that the current concept of the order *Festucetalia valesiacae* is much narrower than that of Braun-Blanquet (1961) who included all dry and semi-dry grasslands of the study area in this order. Whether the *Stipo-Poion xerophilae* can be maintained as an inner-alpine geographical vicariant of the *Festucion valesiacae*, remains to be further investigated.

Among the semi-dry grasslands of the *Brachypodietalia pinnati*, the communities of Styria (*Agrostis capillaris-Avenula adsurgens* community, *Anthericum ramosum-Brachypodium pinnatum* community) clearly belong to the *Cirsio-Brachypodion*, which includes the meadow steppes of eastern Central Europe (Willner et al. 2019). The most important differential species against the western *Bromion erecti* (= *Mesobromion* nom. cons. propos.) is *Festuca rupicola*, which was present with high cover in all relevés. The position of the *Ranunculus bulbosus-Festuca rubra* community and the *Carduus defloratus-Brachypodium pinnatum* community, both observed in the Virgen valley, is less clear. While they do not contain any diagnostic species of the *Mesobromion* (except for a single, probably misclassified relevé from the Inn valley where *Festuca guestfalica* was present), the *Cirsio-Brachypodion* species are also absent in half of the relevés. In fact, the *Carduus defloratus-Brachypodium pinnatum* community is transitional towards alpine grasslands of the *Caricion ferrugineae* (*Elyno-Seslerietea*), and so it even has a marginal position within the class. Finally, the *Astragalo-Brometum* of the Upper Inn valley, originally included in the heterogeneous *Stipo-Poion xerophilae* by Braun-Blanquet (1961), might belong to a hitherto undescribed meso-xeric alliance having its main distribution in the inner-alpine valleys of the Western Alps (and the dealpine gravel plains north and south of the Alps), differentiated against both *Cirsio-Brachypodion* and *Mesobromion* by the high constancy of *Brachypodium rupestre* and *Potentilla pusilla* (see Table 1), which are completely absent from typical stands of either alliance (Dengler et al., in prep.; see Dengler et al. 2020a).

Associations

Perhaps surprisingly, only four clusters could be unambiguously assigned to described associations. The main reason is that a comprehensive syntaxonomic revision of the dry and semi-dry grasslands of the inner Eastern Alps is still lacking. Instead of adopting names of associations that might or might not correspond to our units, we preferred to use informal community names, thus making the insufficient knowledge clearly visible. The relationship between these communities and described associations such as the *Achnathero-Stipetum capillatae* and *Teucrio-Caricetum humilis* (Mucina and Kolbek 1993) could only be clarified in a revision based on all available plot data from the Eastern Alps. For the *Brachypodietalia pinnati* communities, it will be particularly important to include data from Italy and Switzerland, which both were not covered by the revision of Willner et al. (2019). For the syntaxonomic interpretation of the *Festucetalia valesiacae*, a comparison with data from the most continental part of the Eastern Alps, the Vinschgau in South Tyrol (Italy), will be crucial.

Beside the lack of comprehensive studies another reason for the lacking match with associations from the literature might be the unstable management of most of the sites during the last thirty years. Even at sites that have recently become protected under the Natura 2000 regime (like the grasslands of FL and KA in the Upper Inn valley or PÖ in the Mur valley), the current management is very different from the historical, much more intensive use, and it will take quite some time for the vegetation to get in balance with the new type of management.

Our results do not support a closer relationship of the dry and semi-dry grasslands of the Austrian inner-alpine dry valleys with the Pannonian steppes (see Willner et al. 2013), a finding that is also supported by genetic analyses of plant and animal species known from both regions (Kirschner et al. 2020, see paragraph nature conservation below).

Proposed syntaxonomic scheme

Class: *Festuco-Brometea* Br.-Bl. et Tx. ex Klika et Hadač 1944

A. Order: *Stipo pulcherrimae-Festucetalia pallentis* Pop 1968

Alliance: ??? [*Avenulo adsurgentis-Festucion pallentis* Mucina in Mucina et Kolbek 1993 nom. inval. (Art. 3f), "*Diantho lumnitzeri-Seslerion albicantis*" sensu Mucina et Kolbek 1993 p.p.]

Nomenclatural remark: The name *Diantho-Seslerion* (Soó 1971) Chytrý et Mucina 1993 is often used with wrong species

epithets and/or in a way that excludes its type. Neither *Dianthus lumnitzeri* s.str. nor *Sesleria albicans* (= *S. caerulea*) occur in the original diagnosis of the alliance. Soó (1971) described this syntaxon as a suballiance of the *Seslerio-Festucion pallentis* Klika 1931 and listed three associations for it: (1) "*Asplenio rutae-murariae-Melicetum ciliatae*", (2) "*Diantho-Seslerietum heuflerianae-hungaricae*" [≡ *Seslerietum heuflerianae* Zólyomi 1936] and (3) "*Seslerio-Festucetum pallentis*" [≡ *Campanulo divergentiformis-Festucetum pallentis* Zólyomi 1966]. We could not verify if the first association name is valid. However, Borhidi (Borhidi et al. 2012) classifies the *Asplenio rutae-murariae-Melicetum ciliatae* in the alliance *Alysso alyssoidis-Sedion* Oberd. et Müller 1961, so it could hardly be a suitable lectotype. The two other associations, which were both described from the Bükk mountains in Hungary, are often classified in the *Bromo pannonici-Festucion pallentis* Zólyomi 1966 (e.g. Janišová and Dúbravková 2010; Škodová et al. 2015). We are not aware of a published choice of a lectotype for the *Diantho-Seslerion*. It could be argued, that Art. 20 (automatic type) is applicable it this case, but this interpretation needs further confirmation.

A.1 *Armerio elongatae-Potentilletum arenariae* Br.-Bl. 1961

A.2 *Phleo phleoidis-Pulsatilletum nigricantis* Br.-Bl. 1961

A.3 *Medicago minima-Melica ciliata* community

A.4 *Koelerio pyramidatae-Teucrietum montani* Franz in Mucina et al. 1993

B. Order: *Festucetalia valesiacae* Br.-Bl. et Tx. ex Br.-Bl. 1950 nom. cons. propos. [= *Festucetalia* Soó 1940 ≡ *Festucetalia valesiacae* (Soó 1940) 1947 nom. illeg.]

Nomenclatural remark: For the nomenclatural problems surrounding the name *Festucetalia valesiacae* and a formal proposal for a *nomen conservandum*, see Terzi et al. (2017).

Alliance: *Festucion valesiacae* Klika 1931 nom. cons. propos. (= *Festucion sulcatae* Soó 1930; incl. *Stipo-Festucion xerophilae* Br.-Bl. et Richard 1950)

Nomenclatural remark: Kuzemko et al. (2014) proposed to conserve the name *Festucion valesiacae* Klika 1931 against the earlier *Festucion sulcatae* Soó 1930, and this proposal was also adopted by Mucina et al. (2016). However, no formal proposal has been submitted so far.

B.1 *Sempervivum tectorum-Festuca valesiaca* community

C. Order: *Brachypodietalia pinnati* Korneck 1974 nom. cons. propos. (= *Brometalia erecti* Koch 1926)

Nomenclatural remark: Dengler et al. (2003) proposed to reject the name *Brometalia erecti* Koch 1926 as nomen ambiguum, and Kuzemko et al. (2014) proposed to conserve the name *Brachypodietalia pinnati* Korneck 1974. This proposal was also adopted by Mucina et al. (2016), but no formal proposal has been submitted so far.

Alliance: *Cirsio-Brachypodion pinnati* Hadač et Klika in Klika et Hadač 1944

C.1 *Astragalo onobrychidis-Brometum erecti* Br.-Bl. 1950

C.2 *Agrostis capillaris-Avenula adsurgens* community

C.3 *Anthericum ramosum-Brachypodium pinnatum* community

C.4 *Ranunculus bulbosus-Festuca rubra* community

C.5 *Carduus defloratus-Brachypodium pinnatum* community

Biodiversity

For vascular plants, our findings that meso-xeric stands were substantially richer in species than either rocky or xeric grasslands across all grain sizes, is consistent with results from various other regional studies (Dengler et al. 2012, 2019; Pedashenko et al. 2013) as well as a synthesis across the Palaearctic (Dengler et al. 2020b). Our scale-dependent richness values were similar to mean richness from nested-plot sampling in meso-xeric grasslands across the Palaearctic, but about 25% lower in the xeric grasslands and about 40% lower in the rocky grasslands (GrassPlot Diversity Explorer v.2.10; https://edgg.org/databases/GrasslandDiversityExplorer; Biurrun et al. 2021). By contrast, our values for the first two orders (20.0 species for rocky grasslands, 26.9 species for xeric grasslands in 10 m^2) were rather similar to richness data found for such types in the inner-alpine valleys of Italy (Wiesner et al. 2015: 25 species in 10 m^2) and Switzerland (Dengler et al. 2019: 26.3 species for rocky and 24.3 species for xeric grasslands in 10 m^2). Actually, if we exclude the high-elevation associations (transitional to *Elyno-Seslerietea*) of the meso-xeric grasslands also there the richness values were below average and similar to those found in Aosta Valley and Valais (Wiesner et al. 2015; Dengler et al. 2019). While for the Austrian stands one might be tempted to explain the low plot-scale richness with the small size of the majority of remaining patches, this is not the case for the two other regions where there are still large and well-managed dry grasslands persisting. Therefore, we assume that it is rather due to an impoverished species pool in consequence of the glaciations and the isolated position compared to other dry grassland types, but this definitely requires further studies in a broader geographic context, for which the GrassPlot database provides excellent opportunities (Dengler et al. 2018). By contrast, the strong increase of the plot-scale vascular plant species richness with elevation in the meso-xeric order (Table 4, Figure 6: from 27 to 54 species in 10 m^2) is a well-known phenomenon for grasslands of the Alps. Data from the Swiss Biodiversity Monitoring, for example, also show that mean vascular plant species richness across all grassland types increases from 28 via 33 to 44 species in 10 m^2, in the colline, montane and subalpine belts, respectively (Koordinationsstelle Biodiversitäts-Monitoring Schweiz 2009). Specifically, the high species richness in subalpine hay meadows is a well-known phenomenon (Isda 1986; Matouch et al. 2000; Mayer and Grabner 2004).

For bryophytes and lichens, the situation was reversed in comparison to mean values from nested-plot sampling throughout the Palaearctic (GrassPlot Diversity Explorer v.2.10; https://edgg.org/databases/GrasslandDiversityExplorer; Biurrun et al. 2021). Here, the Austrian stands of

the rocky and xeric order were on average nearly twice as rich in species than the Palaearctic average, while in the meso-xeric order we had fewer bryophyte species normally with unclear pattern for lichens in the meso-xeric order. One possible explanation is the large species pool of terricolous cryptogams of open stands from the nearby alpine habitats in case of the first two orders.

Nature conservation

Based on the similar floristic composition of their vegetation, traditional vegetation ecology has anticipated close ties between the inner-alpine dry valleys and the Eastern European steppes (Braun-Blanquet 1961). Such scenarios assume that the biota of inner-alpine steppes are relatively young remnants of the cold-stage steppe belt. In other words, the inner-alpine steppe vegetation was often seen as a young and species poor derivative of the steppe vegetation of Eastern Europe. Genetic data from multiple steppe plants and insects challenged this scenario: The biota of the inner-alpine dry valleys were shown to consist of genetic lineages that have evolved in long-term isolation, and are not closely related to European steppe biota from Central and Eastern Europe (Kirschner et al. 2020). It was also shown that the genetic separation between the biota of inner-alpine and Eastern European steppes did not occur postglacial, i.e. at the beginning of the Holocene, but dates back as early as the mid-Pleistocene epoch (Kirschner et al. 2020). Accordingly, these extrazonal lineages must have survived climate driven range contractions throughout the Pleistocene climate fluctuations, such as during the LGM and the mid-Holocene forest optimum, in isolation, that is in refugia apart from the Pannonian and Eastern European steppes. The palaeoendemic *Sempervivum pittonii* from Gulsen can support these findings. Practically, the isolated nature of Alpine steppe outposts and their previously disregarded genetic uniqueness in respect to the Eastern European steppes raises their conservation value significantly. Adequate management and skilled nature protection activities are key to preserve the inner-alpine steppes and their rich genetic diversity for the future. In this respect, the importance of even small remnants of species-rich grasslands should be pointed out: they are often the last resources for propagules of autochthonous species for restoration projects (Kiehl et al. 2010; Bischoff et al. 2018).

Conclusions and outlook

Our study provides the first phytosociological overview of dry and semi-dry grasslands of the Austrian inner-alpine valleys using new plot data since the seminal work of Braun-Blanquet (1961). While a comprehensive syntaxonomic revision remains a task for future studies, the investigated plots are important references of the current situation. It is obvious that in regions with a still predominantly traditional type of farming, like in the Virgen valley, or in larger continuous areas with a proper management, like in the Nature Park Kaunergrat (Upper Inn valley), biodiversity of grassland-specialists is higher than on smaller grassland parcels within a matrix of high-input agriculture. Regarding the number and cover of red list species, the big serpentinite outcrop Gulsen in the Styrian Mur valley is the leader – without any management, but with very special habitat conditions. With the exceptions of the serpentinite grasslands and former hay meadows on avalanche corridors, all the studied grasslands are depending on a proper management, otherwise they would undergo mostly a natural succession to forests. Many of the grasslands are not only hotspots of biodiversity but also a cultural heritage, some of them maybe for millennia, and therefore have an extraordinarily high conservation value. The results of this study support the importance of grazing animals for achieving conservation targets in species-rich grasslands, as most of the detected biodiversity records are located in grazed habitats.

Data availability

The plot data presented in this paper were recorded on the occasion of the 11th EDGG Field Workshop 2018 in Austria. They are included in the Suppl. material of this paper and are stored in and available from the GrassPlot database (https://edgg.org/databases/GrassPlot; Dengler et al. 2018).

Author contributions

M.M. organized the 11th EDGG Field Workshop and guided it together with H.M. and P.K. As former and current EDGG Field Workshop Coordinators, J.D. and I.D. ensured consistent application of the EDGG methodology. M.M identified critical vascular plant species and led the writing of the manuscript. H.M. identified the lichens and provided information about rare or stenoecious lichens. E.A.K. analysed the soil samples, C.B. identified the bryophytes and added ecological aspects. W.W. prepared the syntaxonomic table and framework, wrote most of the syntaxonomic discussions and revised several other parts of the manuscript, M.J. contributed the descriptions of the *Stipo-Festucetalia pallentis*, J.D. prepared the vegetation tables. P.K. wrote the description of the Upper Inn valley and contributed to the discussion of the nature conservation value. R.G. supported the description of the *Brachypodietalia pinnati* and revised the Introduction. H.R. wrote the description of the Virgen valley. I.D. prepared the map and conducted the inferential statistical analyses, while J.D. wrote the Results and Discussion on biodiversity aspects. All authors revised and approved the whole text.

Acknowledgements

We are grateful to the IAVS for financial support for some of the participants. We would like to give special thanks to Dr. Ernst Partl, director of the Naturpark Kaunergrat for authorizing sampling in the protected areas and for helping with the organization of the field workshop.

References

Aeschimann D, Lauber K, Moser MD, Theurillat JP (2004) Flora alpina. Band 1: *Lycopodiaceae–Apiaceae*. Haupt, Bern, CH, 1159 pp.

Barthlott W, Mutke J, Rafiqpoor D, Kier G, Kreft H (2005) Global centers of vascular plant diversity. Nova Acta Leopoldina Neue Folge 92: 61–83.

Bätzing W (2005) Die Alpen. Geschichte und Zukunft einer europäischen Kulturlandschaft. 3rd edn. Beck, München, DE, 431 pp.

Belonovskaya E, Gracheva R, Shorkunov I, Vinogradova V (2016) Grasslands of intermontane basins of Central Caucasus: land use legacies and present-day state. Hacquetia 15: 37–47. https://doi.org/10.1515/hacq-2016-0016

Bischoff A, Hoboy S, Winter N, Warthemann G (2018) Hay and seed transfer to re-establish rare grassland species and communities: How important are date and soil preparation? Biological Conservation 221: 182–189. https://doi.org/10.1016/j.biocon.2018.02.033

Biurrun I, Burrascano S, Dembicz I, Guarino R, Kapfer J, Pielech R, García-Mijangos I, Wagner V, Palpurina S, …, Dengler J (2019) GrassPlot v. 2.00 – first update on the database of multi-scale plant diversity in Palaearctic grasslands. Palaearctic Grasslands 44: 26–47.

Biurrun I, Pielech R, Dembicz I, Gillet F, Kozub L, Marcenò C, Reitalu T, Van Meerbeek K, Guarino R, …, Dengler J (2021) Benchmarking plant diversity of Palaearctic grasslands and other open habitats. Journal of Vegetation Science 32: e13050.

Borhidi, A, Kevey B, Lendvai G (2012) Plant communities of Hungary. Akadémiai Kiadó, Budapest, HU, 544 pp.

Braun-Blanquet J (1949) Übersicht der Pflanzengesellschaften Rätiens (III). Vegetatio 1: 285–316. https://doi.org/10.1007/BF00184536

Braun-Blanquet J (1961) Die inneralpine Trockenvegetation von der Provence bis zur Steiermark. G. Fischer, Stuttgart, DE, 273 pp.

Braun-Blanquet J (1976) Fragmenta Phytosociologica Rhaetica III, IV und VII. Veröffentlichungen des Geobotanischen Intstituts der ETH, Stiftung Rübel, Zürich 58: 1–44.

Brooks RR (1987) Serpentine and its vegetation: a multidisciplinary approach. Croom Helm, Beckenham, UK, 454 pp.

Buschardt A (1979) Zur Flechtenflora der inneralpinen Trockentäler. Bibliotheca Lichenologica 10: 1–419.

Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. Journal of Vegetation Science 13: 79–90. https://doi.org/10.1111/j.1654-1103.2002.tb02025.x

Dengler J (2008) Pitfalls in small-scale species-area sampling and analysis. Folia Geobotanica 43: 269–287. https://doi.org/10.1007/s12224-008-9014-9

Dengler J, Berg C, Eisenberg M, Isermann M, Jansen F, Koska I, Löbel S, Manthey M, Päzolt J, …, Wollert H (2003) New descriptions and typifications of syntaxa within the project Plant communities of Mecklenburg-Vorpommern and their vulnerability Part I. Feddes Repertorium 114: 587–631. https://doi.org/10.1002/fedr.200311017

Dengler J, Becker T, Ruprecht E, Szabó A, Becker U, Beldean M, Bita-Nicolae C, Dolnik C, Goia I, …, Uğurlu E (2012) *Festuco-Brometea* communities of the Transylvanian Plateau (Romania) – a preliminary overview on syntaxonomy, ecology, and biodiversity. Tuexenia 32: 319–359.

Dengler J, Boch S, Filibeck G, Chiarucci A, Dembicz I, Guarino R, Henneberg B, Janišová M, Marcenò C, Biurrun I (2016) Assessing plant diversity and composition in grasslands across spatial scales: the standardised EDGG sampling methodology. Bulletin of the Eurasian Grassland Group 32: 13–30.

Dengler J, Wagner V, Dembicz I, García-Mijangos I, Naqinezhad A, Boch S, Chiarucci A, Conradi T, Filibeck G, …, Biurrun I (2018) GrassPlot – a database of multi-scale plant diversity in Palaearctic grasslands. Phytocoenologia 48: 331–347. https://doi.org/10.1127/phyto/2018/0267

Dengler J, Widmer S, Staubli E, Babbi M, Gehler J, Hepenstrick D, Bergamini A, Billeter R, Boch R, …, Dembicz I (2019) Dry grasslands of the central valleys of the Alps from a European perspective: the example Ausserberg (Valais, Switzerland). Hacquetia 18: 155–177. https://doi.org/10.2478/hacq-2019-0008

Dengler J, Guarino R, Moysiyenko I, Vynokurov D, Boch B, Cykowska-Marzencka B, Babbi M, Catalano C, Eggenberg S, …, Dembicz I (2020a) On the trails of Josias Braun-Blanquet II: First results from the 12th EDGG Field Workshop studying the dry grasslands of the inneralpine dry valleys of Switzerland. Palaearctic Grasslands 45: 59–88.

Dengler J, Biurrun I, Boch S, Dembicz I, Török P (2020b) Grasslands of the Palaearctic biogeographic realm: introduction and synthesis. In: Goldstein MI, DellaSala DA, DiPaolo DA (Eds) Encyclopedia of the world's biomes. Volume 3: Forests – trees of life. Grasslands and shrublands – sea of plants. Elsevier, Amsterdam, NL, 617–637. https://doi.org/10.1016/B978-0-12-409548-9.12432-7

Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D (1991) Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18: 1–248.

Fischer HS (2015) On the combination of species cover values from different vegetation layers. Applied Vegetation Science 18: 169–170. https://doi.org/10.1111/avsc.12130

Fischer MA, Oswald K, Adler W (2008) Exkursionsflora für Österreich, Liechtenstein und Südtirol. Land Oberösterreich, Linz, AT, 1391 pp.

Flügel HW, Neubauer F (1984) Steiermark. Geologie der österreichischen Bundesländer in kurzgefassten Einzeldarstellungen. Geologische Bundesanstalt, Wien, AT, 127 pp.

Frahm JP, Frey W (2004) Moosflora. Ulmer, Stuttgart, DE, 538 pp.

Frank W, Miller Ch, Pestal G (1987) Geologische Karte der Republik Österreich 1:50.000. 152 Matrei in Osttirol. Geologische Bundesanstalt, Wien, AT.

Franz WR (1988) Zur Soziologie der xerothermen Vegetation Kärntens und des oberen Murtales (Steiermark). Atti del Simposio della Società Estalpino-dinarica di Fitosociologia. Feltre 29 giugno – 3 luglio: 63–88.

Gleirscher P, Pacher M (2005) Griffen und die Altsteinzeit im Südostalpenraum. Rudolfinum – Jahrbuch des Landesmuseums für Kärnten 2004: 65–107.

Grabherr G, Greimler, J, Mucina L (1993) *Seslerietea albicantis*. In: Grabherr G, Mucina L (Eds) Die Pflanzengesellschaften Österreichs. Teil II. Gustav Fischer, Jena, DE, 402–446.

Grims F, Köckinger H (1999) Rote Liste gefährdeter Laubmoose (Musci) in Österreich. In: Niklfeld H (Ed.) Rote Listen gefährdeter Pflanzen Österreichs. Grüne Reihe des Bundesministeriums für Umwelt, Jugend und Familie 10: 153–156.

Gruber A, Pestal G, Nowotny A, Schuster R (2010) Erläuterungen zu Blatt 144 Landeck. In: Geologische Karte der Republik Österreich 1:50.000: Erläuterung. Geologischen Bundesanstalt (Ed), Wien, AT.

Hennekens SM, Schaminée JHJ (2001) Turboveg, a comprehensive data base management system for vegetation data. Journal of Vegetation Science 12: 589–591. https://doi.org/10.2307/3237010

Hill MO (1979) TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Section of Ecology and Systematics, Cornell University, New York, US, 90 pp.

Isda M (1986) Zur Soziologie und Ökologie der *Festuca norica*-Hochgraswiesen der Ostalpen – Phytosociology and ecology of *Festuca norica* – grasslands in the Eastern Alps. Sauteria 1: 239–255.

Janišová M, Dúbravková D (2010) Formalized classification of rocky Pannonian grasslands and dealpine *Sesleria*-dominated grasslands in Slovakia using a hierarchical expert system. Phytocoenologia 40: 267–291. https://doi.org/10.1127/0340-269X/2010/0040-0444

Kiehl K, Kirmer A, Donath TW, Rasran L, Hölzel N (2010) Species introduction in restoration projects – Evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. Basic and Applied Ecology 11: 285–299. https://doi.org/10.1016/j.baae.2009.12.004

Kielhauser GE (1954) Die Trockenrasengesellschaften des *Stipeto-Poion xerophilae* im oberen Tiroler Inntal. Angewandte Pflanzensoziologie, Festschrift Aichinger 1: 646–666.

Kirschner P, Záveská E, Gamisch A, Hilpold A, Trucchi E, Paun O, Sanmartín I, Schlick-Steiner BC, Frajman B, …, Schönswetter P (2020) Long-term isolation of European steppe outposts boosts the biome's conservation value. Nature Communications 11: 1–10. https://doi.org/10.1038/s41467-020-15620-2

Klika J (1933) Studien über die xerotherme Vegetation Mitteleuropas II. Xerotherme Gesellschaften in Böhmen. Beihefte zum Botanischen Centralblatt Dresden 50(2): 707–773.

Kovács JA (1994) A köszegi-hegység és köszeg-hegyalja réttársulásai. In: Bartha D (Ed.) A köszegi-hegység vegetációja [Vegetation of the Köszegi Mountains]. Köszeg-Sopron, HU, 147–174.

Koordinationsstelle Biodiversitäts-Monitoring Schweiz (2009) Zustand der Biodiversität in der Schweiz – Ergebnisse des Biodiversitätsmonitorings Schweiz (BDM) im Überblick. Stand: Mai 2009. Umwelt-Zustand 2009(11): 1–112.

Kuzemko AA, Becker T, Didukh YP, Ardelean IV, Becker U, Beldean M, Dolnik C, Jeschke M, Naqinezhad A, …, Dengler J (2014) Dry grassland vegetation of Central Podolia (Ukraine): a preliminary overview of its syntaxonomy, ecology and biodiversity. Tuexenia 34: 391–430.

Lippert W (1995) Familie *Crassulaceae*, Dickblattgewächse. In: Conert JH, Weber, HE, Jäger EJ, Kadereit JW, Schultze-Motel W, Wagenitz G (Eds) Gustav Hegi. Illustrierte Flora von Mitteleuropa. Band IV Teil 2A, Spermatophyta: Angiospermae: Dicotyledonae 2(2), Blackwell, Berlin, DE, 69–129.

Magnes M (2018) Sonderstandorte in einem inneralpinen Trockental: Spezialisten auf Serpentinit und paläozischen Kalken im oberen Murtal. Tuexenia 11: 113–124.

Magnes M, Mayrhofer H, Kirschner P, Stöhr O, Schwager P, Dengler J, Biurrun I (2018) Invitation and guide to the 11th EDGG Field Workshop grasslands of inneralpine dry valleys: part 1, Eastern Alps, Austria, 6–13 July 2018. Bulletin of the Eurasian Dry Grassland Group 36: 12–25.

Magnes M, Kirschner P, Janišová M, Mayrhofer H, Berg C, Mora A, Afif E, Willner W, Belonovskaya E, …, Dengler J (2020) On the trails of Josias Braun-Blanquet – changes in the grasslands of the inneralpine dry valleys during the last 70 years. First results from the 11th EDGG Field Workshop in Austria. Palaearctic Grasslands 45: 34–58.

Martinovský JO (1970) Über drei neue *Stipa*-Sippen aus dem Verwandtschaftskreis *Stipa joannis* s. l. XXII. Beitrag zur Kenntnis der *Stipa*-Sippen. Österreichische Botanische Zeitschrift 118: 171–181. https://doi.org/10.1007/BF01373228

Matouch S, Traxler A, Grass V (2000) Die Bergmähder des Kärntner Lesachtales - Biodiversität und Nutzungswandel. Carinthia II: 591–604.

Mayer R, Grabner S (2004) Die Vegetation der Bergmähder im Valsertal/Tirol. Tuexenia 24: 227–245.

Melzer H (1962) Neues zur Flora von Steiermark (V). Mitteilungen des Naturwissenschaftlichen Vereines für Steiermark 92: 77–100.

Michor K (1999) Die Virgener Feldflur – eine einzigartige Heckenlandschaft. In: Hochegger K, Holzner W (Eds) Kulturlandschaft – Natur in Menschenhand. Grüne Reihe des Bundesministeriums für Umwelt, Jugend und Familie 11: 460–466.

Mucina L, Kolbek J (1993) *Festuco-Brometea*. In: Mucina L, Grabherr G, Ellmauer T (Eds) Die Pflanzengesellschaften Österreichs. Teil I. Gustav Fischer, Jena, DE, 420–492.

Mucina L, Bültmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, …, Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19(suppl. 1): 3–264. https://doi.org/10.1111/avsc.12257

Niklfeld H, Schratt-Ehrendorfer L (1999) 2. Farn- und Blütenpflanzen. In: Niklfeld H (Ed.) Rote Listen gefährdeter Pflanzen Österreichs. Grüne Reihe des Bundesministeriums für Umwelt, Jugend und Familie 10: 33–152.

Nimis PL, Hafellner J, Roux C, Clerc P, Mayrhofer H, Martellos S, Bilovitz PO (2018) The lichens of the Alps – an annotated checklist. MycoKeys 31: 1–634. https://doi.org/10.3897/mycokeys.31.23568

Oberwalder L (1999) Virgen im Nationalpark Hohe Tauern. Edition Löwenzahn, Innsbruck, AT, 269 pp.

Ozenda P (1988) Die Vegetation der Alpen im europäischen Gebirgsraum. Fischer, Stuttgart, DE, 353 pp.

Patzelt G (1996) Modellstudie Ötztal – Landschaftsgeschichte im Hochgebirgsraum. Mitteilungen der Österreichischen Geographischen Gesellschaft 138: 53–70.

Pedashenko H, Apostolova I, Boch S, Ganeva A, Janišová M, Sopotlieva D, Todorova S, Ünal A, Vassilev K, Dengler J (2013) Dry grasslands of NW Bulgarian mountains: first insights into diversity, ecology and syntaxonomy. Tuexenia 33: 309–346.

Roleček J, Tichý L, Zelený D, Chytry M (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. Journal of Vegetation Science 20: 596–602. https://doi.org/10.1111/j.1654-1103.2009.01062.x

Saukel J, Köckinger H (1999) Rote Liste gefährdeter Lebermoose (Hepatice) und Hornmoose (Anthocerotae) in Österreich. In: Niklfeld H (Ed.) Rote Listen gefährdeter Pflanzen Österreichs. Grüne Reihe des Bundesministeriums für Umwelt, Jugend und Familie 10: 172–186.

Schwabe A, Kratochwil A (2004) *Festucetalia valesiacae* communities and xerothermic vegetation complexes in the Central Alps related to environmental factors. Phytocoenologia 34: 329–446. https://doi.org/10.1127/0340-269X/2004/0034-0329

Schwabe A, Kratochwil A (2012) Die inneralpine Trockenvegetation: von Josias Braun-Blanquet bis zu den "Valori die Bioindicatione" von Sandro Pignatti. Berichte der Reinhold-Tüxen-Gesellschaft 24: 122–139.

Škodová I, Janišová M, Hegedüšová K, Borsukevych L, Smatanová J, Kish R, Píš V (2015) Sub-montane semi-natural grassland communities in the Eastern Carpathians (Ukraine). Tuexenia 35: 355–380.

Soó R (1971) Aufzählungen der Assoziationen der ungarischen Vegetation nach den neueren zönosystematisch-nomenklatorischen Ergebnissen. Acta Botanica Academiae Scientiarum Hungaricae 17: 127–179.

Steinbuch E (1995) Wiesen und Weiden der Ost-, Süd- und Weststeiermark. Dissertationes Botanicae 253: 1–210.

Sydow W (1995) Der hallstattzeitliche Bronzehort von Fließ im Oberinntal, Tirol. Fundberichte aus Österreich, Materialhefte A3: 1–150.

ter Braak JFC, Šmilauer P (2012) Canoco 5. Canoco reference manual and user´s guide. Software for Ordination (version 5). Biometris, Wageningen, České Budějovice, NL, CZ, 496 pp.

Terzi M, Di Pietro R, Theurillat J-P (2017) Proposal (21): to conserve the name *Festucetalia valesiacae* Br.-Bl. & Tx. ex Br.-Bl. 1950 against *Festucetalia* Soó 1940. Phytocoenologia 47: 305–307. https://doi.org/10.1127/phyto/2017/0186

Tichý L (2002) JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Tichý L, Chytrý, M (2006) Statistical determination of diagnostic species for site groups of unequal size. Journal of Vegetation Science 17: 809–818. https://doi.org/10.1111/j.1654-1103.2006.tb02504.x

Theurillat J-P, Willner W, Fernández-González F, Bültmann H, Čarni A, Gigante D, Mucina L, Weber H (2021) International Code of Phytosociological Nomenclature. 4th edn. Applied Vegetation Science 24: e12491. https://doi.org/10.1111/avsc.12491

Türk R, Hafellner J (1999) Rote Liste gefährdeter Flechten (Lichenes) in Österreich. In: Niklfeld H (Ed.) Rote Listen gefährdeter Pflanzen Österreichs. Grüne Reihe des Bundesministeriums für Umwelt, Jugend und Familie 10: 187–228.

Wagner H (1979) Das Virgental/Osttirol, eine bisher zu wenig beachtete inneralpine Trockeninsel. Phytocoenologia 6: 303–316. https://doi.org/10.1127/phyto/6/1979/303

Wiesner L, Baumann E, Weiser F, Beierkuhnlein C, Jentsch A, Dengler J (2015) Scale-dependent species diversity in two contrasting dry grassland types of an inner alpine dry valley (Cogne, Aosta Valley, Italy). Bulletin of the Eurasian Grassland Group 29: 10–17.

Willner W, Tichý L, Chytrý M (2009) Effects of different fidelity measures and contexts on the determination of diagnostic species. Journal of Vegetation Science 20: 130–137. https://doi.org/10.1111/j.1654-1103.2009.05390.x

Willner W, Sauberer N, Staudinger M, Schratt-Ehrendorfer L (2013) Syntaxonomic revision of the Pannonian grasslands of Austria – Part I: Introduction and general overview. Tuexenia 33: 399–420.

Willner W, Roleček J, Korolyuk A, Dengler D, Chytrý M, Janišová M, Lengyel A, Aćić S, Becker T, …, Yamalov S (2019) Formalized classification of semi-dry grasslands in central and eastern Europe. Preslia 91: 25–49. https://doi.org/10.23855/preslia.2019.025

Wirth V, Hauck M, Schultz M (2013) Die Flechten Deutschlands. Band 1, Ulmer, Stuttgart, DE, 672 pp.

ZAMG [Zentralanstalt für Meteorologie und Geodynamik] (2020) Klimadaten von Österreich 1971–2000. http://www.zamg.ac.at/fix/klima/oe71-00/klima2000/klimadaten_oesterreich_1971_frame1.htm [accessed 2 Nov 2020]

E-mail and ORCID

Martin Magnes (Corresponding author, martin.magnes@uni-graz.at), ORCID: https://orcid.org/000-002-5453-5735
Wolfgang Willner (wolfgang.willner@univie.ac.at), ORCID: https://orcid.org/0000-0003-1591-8386
Monika Janišová (monika.janisova@gmail.com), ORCID: https://orcid.org/0000-0002-6445-0823
Helmut Mayrhofer (helmut.mayrhofer@uni-graz.at)
Elías Afif Khouri (elias@uniovi.es)
Christian Berg (christian.berg@uni-graz.at), ORCID: https://orcid.org/0000-0002-0587-3316
Anna Kuzemko (anyameadow.ak@gmail.com), ORCID: https://orcid.org/0000-0002-9425-2756
Philipp Kirschner (philipp.kirschner@gmail.com), ORCID: https://orcid.org/0000-0002-9263-5112
Riccardo Guarino (guarinotro@hotmail.com), ORCID: https://orcid.org/0000-0003-0106-9416
Harald Rötzer (harald.roetzer@a-v-l.at)
Elena Belonovskaya (ebelonovskaya.0709@gmail.com), ORCID: https://orcid.org/0000-0002-8354-4606
Asun Berastegi (aberastg@gan-nik.es), ORCID: https://orcid.org/0000-0003-0456-3305
Idoia Biurrun (idoia.biurrun@ehu.eus), ORCID: https://orcid.org/0000-0002-1454-0433
Itziar Garcia Mijangos (itziar.garcia@ehu.eus), ORCID: https://orcid.org/0000-0002-6642-7782
Ermin Mašić (erminmasic@hotmail.com), ORCID: https://orcid.org/0000-0001-5383-2431
Jürgen Dengler (dr.juergen.dengler@gmail.com), ORCID: https://orcid.org/0000-0003-3221-660X
Iwona Dembicz (i.dembicz@gmail.com), ORCID: https://orcid.org/0000-0002-6162-1519

Supplementary material

Supplementary material 1
Geographic, environmental and structural data of the analysed plots (pdf)
Link: https://doi.org/10.3897/VCS/2021/68594.suppl1

Supplementary material 2
Complete, sorted relevé and synoptic table (pdf)
Link: https://doi.org/10.3897/VCS/2021/68594.suppl2